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HYDROGEN ION CONCENTRATION IN RELATION TO ECOLOGICAL FACTORS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 307

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(WITH FOURTEEN FIGURES)

Introduction

Neither space nor other circumstances warrant even a brief review of the many theories of soil acidity. AMES and SCHOLLENBERGER (1), FREAR (8), HARRIS (10), MIRASOL (13), and TRUOG (20) have reviewed the most prominent theories of soil acidity before the modern H-ion concentration theory was applied to soil solutions. The latter conception is discussed by ATKINSON (3), CLEMENTS (4), FISHER (7), GILLESPIE (9), SHARP and HOAGLAND (19), and WHERRY (25, 27). Such investigators as COVILLE (5), FERNALD (6), HILGARD (11), HUTCHINSON and MACLENNAN (12), SALISBURY (16), SAMPSON (18), and others have observed relationships between soil acidity and the distribution of natural vegetation, but in none of this work was the H-ion concentration considered.

In a series of papers beginning with 1916, WHERRY (21, 22, 23, 24, 27) describes a surprising correlation between many plant species and H-ion concentration. He determined the acidity with a set of colorimetric indicators, and worked extensively in some of the eastern Atlantic and New England states. ARRHENIUS (2), making an intensive physico-ecological study of some of the Stock-

holm Schären (small islets), speaks of similar relation between H-ion concentration and plant associations. OLSEN (**14**) in Denmark also made an intensive physico-ecological investigation of physical and chemical factors, and similarly concluded that the H-ion concentration is important in determining the character of the vegetation. ATKINSON (**3**) also has found a correlation between H-ions and the distribution of a number of species. SALISBURY (**17**) considers the P_H an important factor in determining the distribution of woodland species and plant successions.

From the foregoing it is evident that the H-ion concentration has received considerable attention as an ecological factor, but some phases have scarcely been touched. The writer knows of no serious attempt to obtain data on the relationship between H-ion concentration and topography. Very little is known of the downward gradient of acidity from surface to subsoils. WHERRY (**24**) and ARRHENIUS (**2**) have observed such relationships, but give little data. PLUMMER (**15**) records H-ion concentration data of surface and subsoils from the southeastern states, but he used variable depths to represent the two layers of soil. SALISBURY (**17**) has made a stratificational study of the P_H in woodland soils, but only to a depth of nine inches.

In a private communication WHERRY described a few seasonal observations made of a swamp near Washington, D.C., and SALISBURY determined the acidity of the "same spot" in a *Quercus Robur* association in the spring and summer. The writer knows of no other similar observations. Having in mind these several phases, the present investigator, whose results are recorded here, aimed to carry out studies that would show: (1) the general influences of topography, soil types, soil depths, and seasonal phenomena on the H-ion concentration; and (2) the latter as a factor in plant distribution.

Method

In determining the H-ion concentration, WHERRY'S latest modified field method (**27**) was used. For collecting the soil samples, a Brightwood soil auger 1.5 inches in diameter, 40 inches long, and marked at 6-inch intervals was found to be satisfactory. Since a few grams suffice for a test, one can easily secure samples

from any depth and remove uncontaminated inner portions of the soil from the tip of the auger. In cases where the soil was saturated with water, parallel holes to the depths desired were bored and the samples obtained quickly. In this way it is believed serious contaminations from higher strata were avoided. Whenever data of individual species were sought, the tests were made at once in the field, but in other phases of the work, where many samples were needed, the soils were collected in small 8 cc. bottles. Excepting some highly colloidal or turbid solutions, to which reference will be made again, the tests were all made within twenty-four hours. The solutions were always kept standing in temperatures comparable with those in the field. The writer has checked up by making tests on similar samples in the field, and twenty-four hours later in the laboratory. Within the degree of accuracy which WHERRY'S method permits, the results were found to be identical.

A rich mesophytic woodland in which circumneutral reactions are the most abundant may have many local patches of high acidity. Such occurrences are common at the base of trees, in very much decayed logs, or in moist soils with a high organic content. In fact, appreciable fluctuations will occur almost anywhere. For that reason care must be taken in selecting samples. In order to secure typical data the writer chose spots that were representative from a vegetational aspect. In addition, the following precaution was taken: (1) samples tested from the roots of species near the boring; (2) results checked by parallel holes; (3) holes made in close series, as at the Baroda or Chesterton bogs; or (4) work repeated, as at Starved Rock, all the dunes sites, and Thornton.

Discussion of figures

In the figures the profiles represent the topography, and the straight lines with cross marks represent the borings, each interval denoting six inches. The H-ion is expressed in terms of specific reaction, as used by WHERRY (**21**). Briefly, WHERRY considers the acidity or alkalinity of water as unity. In round numbers a solution is then 3, 10, 30, 100, 300 . . . . times as acid or alkaline as water. Specific acidities of 1, 3, 10, 30, 100, 300, 1000 . . . . correspond to P_H values of 7, 6.5, 6, 5.5, 5, 4.5, 4 . . . . respectively; and specific alkalinities of 1, 3, 10, 30, 100 . . . . corre-

spond to P_H values of 7, 7.5, 8, 8.5, 9. . . . . In the figures of this paper specific alkalinities will be distinguished by *italicised* numbers. The water table, whenever it was reached, is indicated by *WT*. Height has reference to the approximate vertical distance from the immediate lowland or floodplain to the upland. The angle of the slope is estimated from the horizontal. Habitats are labelled by capital letters, so that in reading the legends one can at the same time see some of the relationships of H-ion concentration to topography, soil stratification, types of soil, and plant distribution. While a list of plants is given for each habitat, it is not the intention to group these species around certain H-ion concentrations. For the most parts the lists are incomplete, only the conspicuous forms being noted. Moreover, at the time some samples were collected only certain species were identifiable.

Thornton Forest Preserve

The Thornton Forest Preserve is 25 miles south of Chicago on the Chicago and Eastern Illinois Railroad. Most of the topography is flat, having formerly been the bed of the present Lake Chicago which antedated Lake Michigan. Thorn Creek traverses the preserve in a northerly direction. To the west of the creek the glacial drift is exposed. The soils are sandy loams, merging downward into silt or clay loams, and clays. On the east side the drift is overlain by about 3 feet of fine depositional sand. About a mile east the flat topography is interrupted by a north-south sand ridge, which is an old beach remnant covered with coarse dune sand, its brown color probably being due to iron oxides.

In studying the profiles one notes that the floodplains are slightly acid, neutral, or even alkaline; that the uplands are more acid; and that the acidity of the undrained flatwoods, parts of the meadow, and of the small depression in the beach is especially and consistently high. The flat topography, the impermeable clayey drift underlying the sand, together with a dense stand of trees make conditions ideal for soil saturation and a consequent acidity. How far down it is to the clay in the beach depression could not be determined with a 3-foot auger. At any rate, the sand is high in organic matter, saturated, and highly acid. The meadow *M*, *M*[1] to the north of the acid woods *D–I* (fig. 1) was formerly

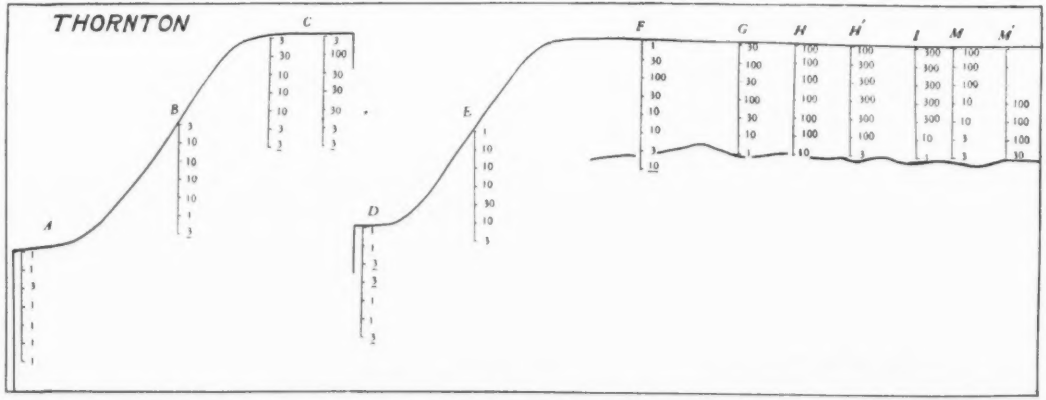

FIG. 1.—Thornton Forest Preserve: *A*, floodplain 50 feet wide, with sandy clay soil merging below into pure clay; SPECIES: *Quercus alba, Q. rubra. Ulmus americana, Crataegus* sp., *Fraxinus americana, Urtica dioica, Ranunculus septentrionalis, Arabis laevigata, Agrimonia parviflora, Viola cucullata, Circaea lutetiana, Sanicula marilandica, Cryptotaenia canadensis, Lappula virginiana, Pentstemon laevigatus, Campanula americana, Lobelia siphilitica. B*, west facing slope, angle 45°; with glacial clay soil; SPECIES: *Uvularia grandiflora, Erythronium albidum, Smilacina racemosa, Sanguinaria canadensis, Phlox divaricata. C*, upland, about 100 feet from *A*; height 20 feet; sandy loam soil merging below into silt and clay loams; SPECIES: *Carya ovata. Quercus alba, Q. rubra, Pyrus coronaria, Tilia americana, Smilacina racemosa, Smilax herbacea, Silene stellata, Anemone virginiana, Geum album, Geranium maculatum, Polemonium reptans, Veronica virginica, Galium concinnum, Rudbeckia hirta. D*, floodplain of Thorn Creek, about 300 yards east of *A;* sandy clay soil; SPECIES: *Fraxinus americana, Ribes cynosbati, Psedera quinquefolia, Sambucus canadensis, Ranunculus septentrionalis, Sanicula marylandica, Osmorhiza longistylis, Cryptotaenia canadensis, Galium concinnum, Ambrosia trifida, Rudbeckia laciniata. E*, west facing slope, angle 45°; sandy clay soil merging into clay; SPECIES: *Quercus alba, Q. rubra, Acer rubrum, Fraxinus americana, Smilax herbacea, Sambucus canadensis, Luzula campestris, Smilacina racemosa, Arenaria lateriflora, Ranunculus abortivus, R. septentrionalis, Anemone caroliniana, Oxalis violacea, Geranium maculatum, Monarda fistulosa, Galium concinnum. F*, upland, height 30 feet; soil 3 feet of fine sand underlain by drift; SPECIES: *Carya ovata, Quercus alba, Q. rubra, Q. ellipsoidalis, Prunus virginiana, Pyrus melanocarpa, Luzula campestris, Smilacina racemosa, Comandra umbellata, Claytonia virginica, Podophyllum peltatum, Fragaria virginiana, Geum album, Agrimonia parviflora, Oxalis violacea, Monarda fistulosa, Antennaria plantaginifolia, Achillea Millefolium. G*, clearing of several acres about 200 yards from *F;* soil as at *F;* SPECIES: *Aspidium thelypteris, Equisetum arvense, Luzula campestris, Maianthemum canadense, Smilacina racemosa, Fragaria virginiana, Potentilla canadensis, Geranium maculatum, Viola fimbriatula, Houstonia caerulea, Achillea Millefolium. H, H'*, several acres of forest burned over about 1916, secondary succession coming in; *H*, 50 feet from main woods, *H'*, 300 feet away; soil as at *F* and *G;* SPECIES: *Populus grandidentata, P. tremuloides, P. deltoides, Salix petiolaris, Marchantia polymorpha, Polytrichum commune, Pteris aquilina, Spiranthes cernua, Salix glaucophylla, Ludvigia polycarpa, Epilobium adenocaulon, Steironema ciliatum, Solidago* spp., *Aster* spp., *Aster paniculata. I*, "acid flat woods," proper; soil as preceding; SPECIES: *Quercus alba, Q. rubra, Q. ellipsoidalis, Sassafras variifolium, Nyssa sylvatica, Pyrus melanocarpa, Gaylussacia baccata, Vaccinium pennsylvanicum, Sphagnum, Pteris aquilina, Aspidium thelypteris, Aspidium spinulosum, Osmunda regalis, Osmunda cinnamonea, Maianthemum canadense. M*, meadow 50 feet north of the flatwood boundary; soil as preceding; SPECIES: *Baptisia leucantha, Polygala sanguinea, Ludvigia polycarpa, Phlox glaberrima, Prunella vulgaris, Pycnanthemum lanceolatum, Lycopus americanus, Veronica* sp., *Veronica virginica, Eupatorium perfoliatum, Rudbeckia hirta, Helianthus mollis, Coreopsis tripteris. M'*, *Spiraea latifolia, Vaccinium pennsylvanicum, Pteris aquilina, Maianthemum canadense, Habenaria ciliaris, Baptisia leucantha, Polygala sanguinea, Ludvigia polycarpa, Eupatorium perfoliatum, Liatris spicata, Erigeron annuus, Parthenium integrifolium, Coreopsis tripteris.*

part of the forest, but has been farmed and since abandoned. Whether the high acidity is residual, or is independent of the old forest was not determined. In contrast with this there is the low acidity of the meadow to the west of the second acid flatwood *A–O*.

Excepting in the floodplains one sees a general downward diminution of acidity. This gradient is usually gradual and may change to definite alkalinity if the underlying pure clays are reached. The effect of drainage on acidity is shown by the ravines and the uplands nearby. In the ravine slopes, however, we have both drainage and exposure of glacial till lessening the acidity. If the slope is a gradual north-facing one, covered with eroded sand as slope *J*, *K*, *L* (fig. 2) for instance, the acidity even there may be appreciable. The small ravine at *J* (fig. 2) has cut 10–15 feet into the underlying drift, but washed-in sands result in a sandy loam, so that here there is a slight acid instead of neutrality or slight alkalinity, as in the case of the other ravine bottom where clays predominate. Notable also is the fact that the burned over area where some *Marchantia polymorpha* and *Epilobium adenocaulon* are still hanging on shows very little diminishing of acidity at this time.

The legends show that a number of species which occur in the loams of glacial origin on the west side of the creek grow also in the sands on the east side. On the other hand, in the sandy acid flatwood of high acidity we find *Sassafras variifolium*, *Nyssa sylvatica*, *Gaylussacia baccata*, *Vaccinium pennsylvanicum*, *Sphagnum*, *Pteris aquilina*, *Aspidium thelypteris*, *Osmunda regalis*, *Osmunda cinnamomea*, *Maianthemum canadense*, *Pyrus melanocarpa;* in the sandy meadow of low acidity, *Viola lanceolata*, *Houstonia caerulea;* in the sandy meadow of high acidity, *Pteris aquilina*, *Maianthemum canadense*, *Spiraea tomentosa*, *Vaccinium pennsylvanicum;* on the beach of a medium acidity, *Pteris aquilina*, *Lupinus perennis*, *Viola pedata*, *Vaccinium pennsylvanicum*, *Phlox glaberrima*, *Artemisia canadensis*. Not one of these grows on the west side of the creek.

The data will show that the acidity of the beach (fig. 1 *R*) and the upland of the west side (fig. 1 *C*, *C*[1]) are essentially the same; the acidity of the one meadow (fig. 2 *N*) is about that of the west side upland.

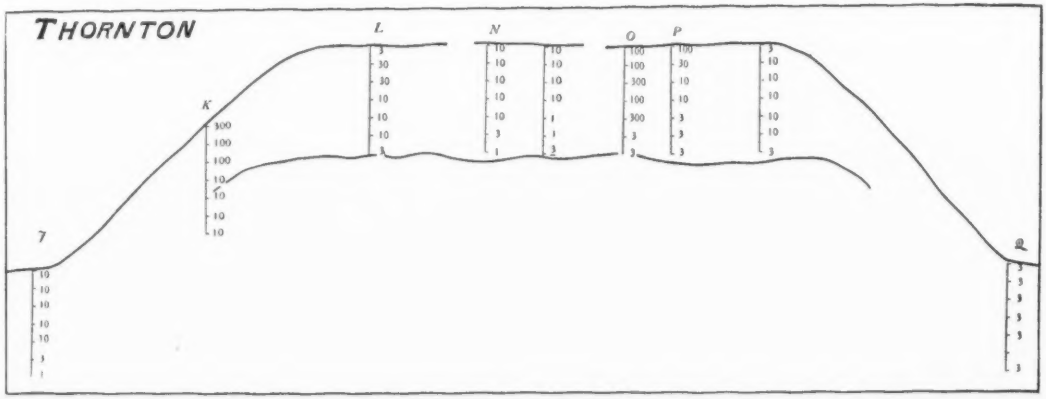

FIG. 2.—*J*, *K*, *L:* one side of east-west ravine through acid flatwoods. *J*, tiny floodplain; sandy loam soil; SPECIES: *Salix* sp., *Populus deltoides*, *P. tremuloides*, *Fraxinus americana*, *Sambucus canadensis*, *Ranunculus septentrionalis*, *Viola cucullata*, *Sanicula marilandica*, *Osmorhiza longistylis*, *Phlox divaricata*, *Ambrosia trifida*, *Rudbeckia laciniata*. *K*, north facing slope, angle 30°; soil sand underlain by clay; SPECIES: *Sassafras variifolium*, *Pyrus coronaria*, *Corylus americana*, *Rubus* sp., *Vaccinium pennsylvanicum*, *Pteris aquilina*, *Smilacina racemosa*, *Solidago* sp., *Antennaria plantaginifolia*. *L*, ridge 18 feet high; soil sand underlain by drift at 3 foot level; SPECIES: *Quercus alba*, *Q. rubra*, *Sassafras variifolium*, *Pyrus coronaria*, *Pteris aquilina*, *Geranium maculatum*. *Q*, *P*, *O*, ravine of another acid flatwoods area about 1 mile southwest of acid woods considered in fig. 1; soil same as at *F–I* (fig. 1). *Q*, floodplain 50 feet wide; sandy clay soil becoming clay at bottom; SPECIES: *Pyrus coronaria*, *Prunus serotina*, *P. virginiana*, *P. americana*, *Vitis* sp., *Sambucus canadensis*, *Pilea pumila*, *Viola cucullata*, *Sanicula marilandica*, *Triosteum perfoliatum*, *Ambrosia trifida*. *P*, upland 25 feet high, 200 yards from *Q;* SPECIES: *Quercus alba*, *Q. rubra*, *Q. ellipsoidalis*, *Pyrus melancarpa*, *Rubus* sp., *Smilacina racemosa*, *Geranium maculatum*, *Viola cucullata*, *V. fimbriatula*. *O*, same level as *P*; soil same; SPECIES: *Sassafras variifolium*, *Spiraea tomentosa*, *Pyrus melanocarpa*, *Vaccinium pennsylvanicum*, *Sphagnum*, *Pteris aquilina*, *Maianthemum canadensis*, *Gaylussacia baccata*. *N*, meadow 600 yards west of *P;* soil same; SPECIES: *Equisetum arvense*, *Potentilla canadensis*, *Viola fimbriatula*, *V. lancolata*, *Houstonia caerulea*, *Senecio aureus*.

The H-ion concentration of the flatwoods and of the meadow at M and M^1 (fig. 1) is considerably higher than the west side upland, but here too disturbing factors enter, for *Vaccinium pennsylvanicum*, *Maianthemum canadense*, *Pteris aquilina*, *Sassafras variifolium* grow also on the beach. In fact, as will be shown later, these three species grow in alkaline sands. It would seem, therefore, that H-ion concentration per se is not the only limiting factor.

Palos Park

A series of borings was made at the Palos Park Forest Preserve about 20 miles southwest of Chicago. The particular ridge studied (fig. 3 *A*, *B*, *C*) is part of the Valparaiso moraine. Its north slope faces a wide floodplain of the Sag, which was a former outlet of Lake Chicago.

The rugged topography of Palos Park contrasts sharply with the flat till of Thornton, but in general the plant associations of the glacial soils of the two localities do not differ markedly. Both places show a downward gradient of H-ion, an acid upland, and a neutral or circumneutral floodplain.

Apple River Canyon

The Apple River Canyon area studied lies in Rush Township, Jo Daviess County, northwestern Illinois. This region is part of the famous driftless area which has escaped glaciation. Three geological strata occur here: the Galena dolomite which outcrops in the canyons; the locally overlying Maquoketa shale which in places is covered by loess; and the Niagara dolomite which caps the higher erosion remnants of the shale. Benton Mount nearby, which rises about 200 feet above the surrounding country, is an example of a thick bed of the shale overlaid by Niagara limestone and dolomite.

The rocky talus slopes of the canyons offer a soil that is usually only about a foot in depth, yet some of these slopes have attained a high degree of mesophytism. For the sake of continuity from floodplain to upland, however, slopes had to be chosen that were not typical of the luxuriant vegetation. Tests made on many individuals in all possible crags and crannies, however, indicated that the reactions obtained for the talus slopes are typical.

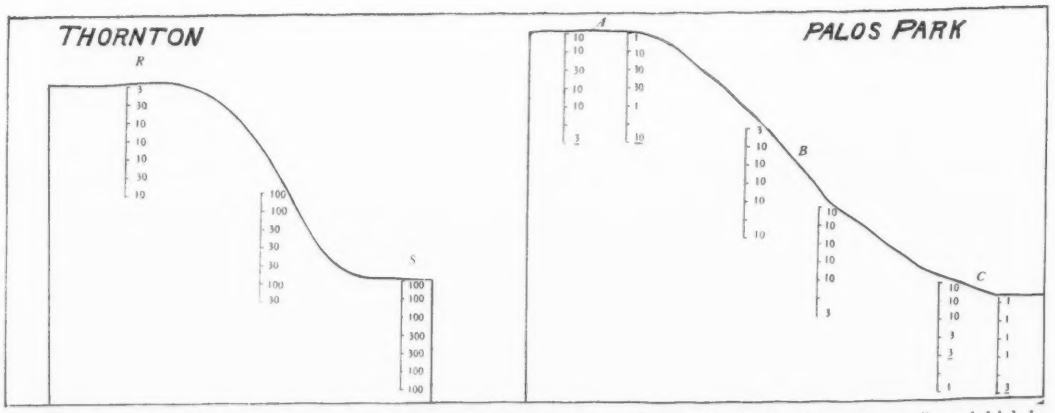

FIG. 3.—*S, R:* old beach one mile east of flatwoods (*F–I*, fig. 1). *S*, depression about 50×100 feet; soil sand, high in organic matter; SPECIES: *Salix glaucophylla, Aspidium thelypteris, Osmunda regalis.* *R*, about 8 feet high; soil brown coarse sand, humus layer about 0–6 inches; SPECIES: *Quercus alba, Q. rubra, Q. ellipsoidalis, Q. velutina, Vaccinium pennsylvanicum, Pteris aquilina, Smilacina racemosa, Maianthemum canadense, Silene stellata, Lupinus perennis, Viola pedata, Phlox pilosa, Rudbeckia hirta.* *A*, morainic upland, height about 100 feet; silt or clay loam soil; SPECIES: *Quercus alba, Q. rubra, Carya ovata, Acer saccharum, Fraxinus americana, Claytonia virginiana, Potentilla canadensis, Viola cucullata, Myosotis virginica, Nepeta Cataria, Monarda fistulosa, Hedeoma hispida, Veronica serpyllifolia, Erigeron pulchellus, Achillea Millefolium.* *B*, north facing slope, angle 40°; silt or clay loam soil; SPECIES: *Ostrya virginiana, Quercus alba, Q. rubra, Acer saccharinum, Tilia americana, Cystopteris fragilis, Arisaema triphyllum, Erythronium albidum, Pilea pumila, Claytonia virginica, Ranunculus abortivus, R. septentrionalis, Hepatica triloba, Actaea alba, Dicentra Cucullaria, Dentaria laciniata, Potentilla canadensis, Floerkea proserpinacoides, Osmorhiza longistylis, Phlox divaricata, Hydrophyllum appendiculatum, Nepeta Cataria.* *C*, more or less open grassland; clay loam soil; SPECIES: *Acer saccharinum, Crataegus* sp., much grass, *Symplocarpus foetidus, Ranunculus abortivus, Erigeron pulchellus.*

Whether the clays at *C* and *E* (fig. 4) are residual or loess the writer does not know; at any rate the acidity of the upland, although slight, is again in contrast with the alkalinity or neutrality of the floodplain. Downward gradients also are evident. There is also a slight tendency toward acidity on Benton Mount in a soil of calcareous origin.

Starved Rock State Park

This study concerns itself with several canyons of Starved Rock State Park, La Salle County, Illinois. In this region the Illinois River runs in an east-west direction and the canyons join to it from the south. St. Peter sandstone constitutes the rock of these canyons. In the neighborhood of Tonti, La Salle, and Hennepin canyons where the borings were made, the sandstone is overlain successively by Pottsville clays, Carbondale shales, coal beds, and glacial drift. For the most part these overlying formations may be neglected, since they are mantled almost entirely by a layer of wind blown or water deposited clay[1] of glacial origin.

As observed elsewhere, the floodplains here also are neutral or even alkaline (fig. 5), and the uplands (fig. 6) acid. The neutrality of these floodplains doubtless is tied up with the alkalinity of the running water. Quite in contrast with the soils studied hitherto, there is no general downward gradient of acidity; in some cases the lower depths show actual increases. It will also be noticed that the lower slopes of the upland are more acid than the peaks. These relationships are somewhat puzzling and interesting. More interesting is the distribution of some species. The acidity of the upland clays is essentially the same as that of the raw sandy slopes, yet many characteristic plants of the latter are absent from the former. Only here and there do *Vaccinium pennsylvanicum* and *Gaylussacia*

[1] Some of these highly acid clays (specific acidity 30–100) had a high suspension content that required about a week for settling. Bromthymol blue, bromcresol purple, and methyl red turned yellow at once when the turbid soil solutions were added, so that it was not possible to make even approximately correct determinations in 24 hours. The tests were therefore made at the end of a week. Just a few of the highly acid soil solutions cleared within 24 hours, and these were tested then and again a week later with the same result. Whether or not the H-ion concentration of the turbid clay solutions would likewise not change appreciably is a matter of conjecture. The writer believes, however, that the data thus obtained are approximately correct.

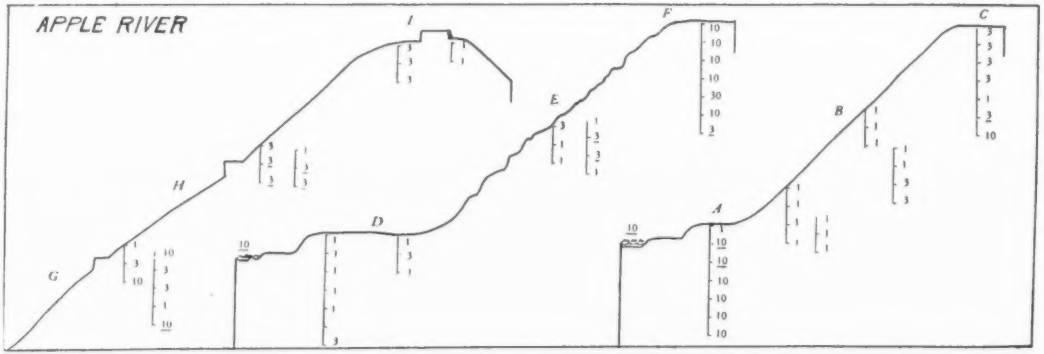

FIG. 4.—*A*, floodplain of tributary canyon; soil alluvial and dolomitic rock fragments; grass. *B*, south facing slope, angle 30°; soil shallow and of dolomitic origin; SPECIES: *Juglans cinerea, Ostrya virginiana, Carpinus caroliniana, Zanthoxylum americanum, Acer saccharum, Corylus americana, Exonymus atropurpurea, Vitis* sp., *Cystopteris fragilis, Trillium recurvatum, Claytonia virginica, Hepatica triloba, Isopyrum biternatum, Sanguinaria canadensis, Dicentra cucullaria, Dentaria laciniata, Fragaria virginiana, Impatiens* sp., *Hydrophyllum* sp., *Monarda fistulosa*. *C*, upland meadow, 80 feet high; soil probably loess; SPECIES: mosses, *Rumex acetosella, Cerastium arvense, Lepidium virginicum*. *D*, floodplain of main canyon, about 200 feet wide; SPECIES: *Quercus alba, Q. rubra, Ulmus fulva, Prunus serotina, Robinia pseudo-Acacia, Fraxinus americana, Cryptogramma acrostichoides, Cystopteris bulbifera, Allium tricoccum, Erythronium albidum, Claytonia virginica, Isopyrum biternatum, Podophyllum peltatum, Osmorhiza longistylis, Polemonium reptans, Monarda fistulosa*. *E*, west facing slope, angle 45°; soil clay and dolomitic fragments; SPECIES: *Carya ovata, Quercus alba, Q. rubra, Prunus serotina, Robinia* pseudo-*Acacia, Cystopteris bulbifera, Smilacina* sp., *Cerastium arvense, Hepatica triloba, Sanguinaria canadensis, Mitella diphylla*. *F*, grazed upland, height 200 feet; soil probably loess; SPECIES: *Rhus typhina*, mosses, *Luzula campestris, Ranunculus fascicularis, Anemone* sp., *Dodecatheon Meadia, Monarda fistulosa, Antennaria plantagifolia*. *G, I*, xerophytic north facing slope of Benton Mount about 1.5 miles from canyon, angle 35°; soil shallow clay of Niagra dolomitic origin. *G*, grass. *H*, grass, *Corylus americana, Monarda fistulosa*. *I*, *Quercus macrocarpon, Corylus americana, Prunus americana, Nepeta Cataria, Monarda fistulosa, Verbascum thapsus*.

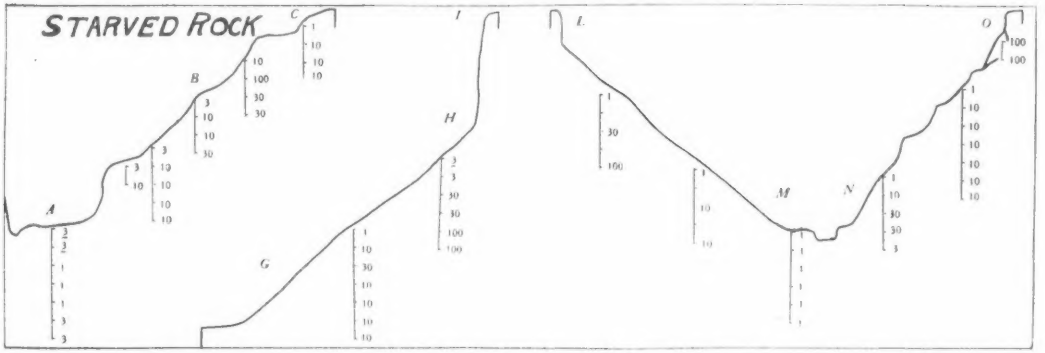

FIG. 5.—*A*, floodplain of Tonti canyon, about 25 feet wide; soil loam; SPECIES: *Carex* sp., *Salix* sp., *Ulmus americana*, *Pilea pumila*, *Acer saccharinum*, *Plantago major*, *Aster* sp. *B*, rocky north facing slope of Tonti Canyon; height 80 feet; slope 35°; soil disintegrated, substratum St. Peter sandstone rock; SPECIES: *Pinus Strobus*, *Juniperus virginiana*, *Rubus* sp., *Gaylussacia baccata*, *Vaccinium pennsylvanicum*, mosses, *Polypodium vulgare*, *Aspidium marginale*, *Osmunda claytoniana*, *Osmunda regalis*, *Maianthemum canadense*, *Pedicularis lanceolata*, *Mitchella repens*. *G*, *H*, talus slope at base of north facing cliff just west of mouth of Hennepin Canyon, cliff 80 feet high, slope 20 feet high, angle 30°; soil silty clay loam; SPECIES: *Carya ovata*, *Juglans cinerea*, *J. nigra*, *Quercus alba*, *Q. rubra*, *Ulmus americana*, *Hamamelis virginiana*, *Prunus serotina*, *Cercis canadensis*, *Tilia americana*, *Fraxinus americana*, *Hydrangea arborescens*, *Psedera quinquefolis*, *Sambucus canadensis*, *Uvularia grandiflora*, *Erythronium albidum*, *Trillium erectum*, *T. grandiflorum*, *Claytonia virginica*, *Hepatica triloba*, *Sanguinaria canadensis*, *Dicentra Cucullaria*, *Gymnocladus dioica*, *Erigenia bulbosa*. *M*, *N*, floodplain of Hennepin Canyon, about 50 feet wide; soil clay loam; SPECIES: *Carpinus caroliniana*, *Ulmus fulva*, *Hamamelis virginiana*, *Robinia pseudo-Acacia*, *Acer Negundo*, *Tilia americana*, *Fraxinus americana*, *Evonymus atropurpureus*, *Sambucus canadensis*, *Pilea pumila*, *Boehmeria cylindrica*, *Agrimonia parviflora*, *Impatiens pallida*, *Osmorhiza longistylis*, *Campanula americana*, *Lobelia siphilitica*. *L*, *M*, and *N*, *O*, east and west facing slopes respectively of Hennepin Canyon, height about 40 feet; soil sands at *N*, *O*, and sand clay mixtures at *L*, *M*; SPECIES: *Carya ovata*, *Carpinus caroliniana*, *Quercus rubra*, *Prunus serotina*, *Hydrangea arborescens*, *Sambucus canadensis*, mosses, *Polypodium vulgare* (chiefly on sands of slope *N*, *O*), *Aspidium marginale*, *A. spinulosum*, *Claytonia virginica*, *Hepatica triloba*, *Aquilegia canadensis*, *Osmorhiza longistylis*.

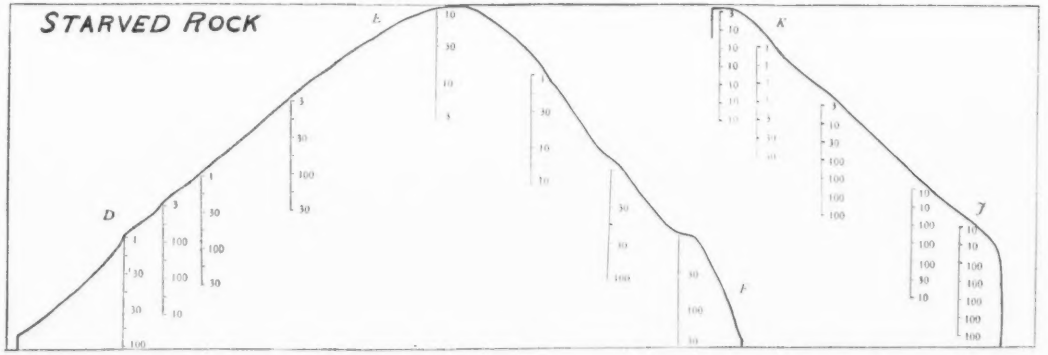

FIG. 6.—*D, E, F,* clay upland included in the "*U*" or horseshoe which formed by joining of Tonti and La Salle Canyons *D, E,* continuation of slope *A, C* (fig. 5); height from *C,* 60 feet; angle 30°; soil clay, substratum Pottsville clays, shales, drift, etc.; SPECIES: *Carya ovata, Quercus alba, Q. velutina, Ribes* sp., *Cassia Chamaecrista, Baptisia leucantha, Monarda fistulosa, Veronica virginica, Erigeron annuus, Rudbeckia hirta. E, F,* south facing slope, corresponding to *D, E,* and continuation of south facing slope of La Salle Canyon; soil and vegetation comparable with slope *D, E. J, K,* clay upland and continuation of cliff *H, I* (fig. 5); height about 50 feet from top of cliff; angle 30°; soil substratum and vegetation similar to *D, E, F* (fig. 6).

migrate a few feet into the acid clays from the sand below. As at Thornton, we find that acid clay and acid sand habitats may be characterized by very different plant associations. The talus slopes do not differ widely one from the other in acidity, but they do differ in the nature of their soils and vegetation. For example, the soil of slope *B*, *C* (fig. 5) is a raw sand, while that of slope *H*, *I* (fig. 6) is a silty clay loam. *Vaccinium*, *Gaylussacia*, species of *Osmunda* grow on the former, and *Trillium*, *Dicentra*, *Arisaema*, *Erythronium*, *Claytonia*, *Sanguinaria*, *Ranunculus*, etc., on the latter.

Long Lake Dunes

The Lake Michigan dunes were investigated in three localities, Long Lake and Mineral Springs, Indiana, and Sawyer, Michigan. That dunes are essentially hills of sand swept landward by prevailing off-shore winds is pretty generally known. Even a short geological discussion seems therefore unnecessary. The Long Lake dunes will be considered first. The highest of these are about 150 feet high, but those studied did not exceed 100 feet. Of outstanding interest is the fact that the younger sand deposits are definitely alkaline. Although in general this alkalinity is replaced by acidity as we proceed landward, it may persist in places half a mile or more from the lake. The high alkalinity (*10–30*) of the lake water indicates a high content of bases. Naturally enough these bases accompany the sand washed ashore by the waves.

Another feature is the occurrence of certain species on these alkaline sands. *Pinus Banksiana*, which FERNALD says "is confined to acid soils," occurs here in abundance. *Arctostaphylos uva-ursi* is abundant also, and grows in soils reaching a specific alkalinity of *10*. *Chimaphila umbellata* is rare; one plant was found, and that one in sand of specific alkalinity *10*.

The habitat F^1 (fig. 8) proved to be a surprise, for the only colony of *Vaccinium macrocarpon* encountered in these dunes grew in this typically neutral spot. Off to one side a little higher under *Pinus Banksiana* were found also *Pyrola secunda*, *Linnaea borealis* var. *americana*, *Arenaria stricta*, and *Maianthemum canadense*. The soils of all these plants ranged from *3* to *3*. Locally a patch of decayed wood gave a specific acidity of 300. *Cornus*

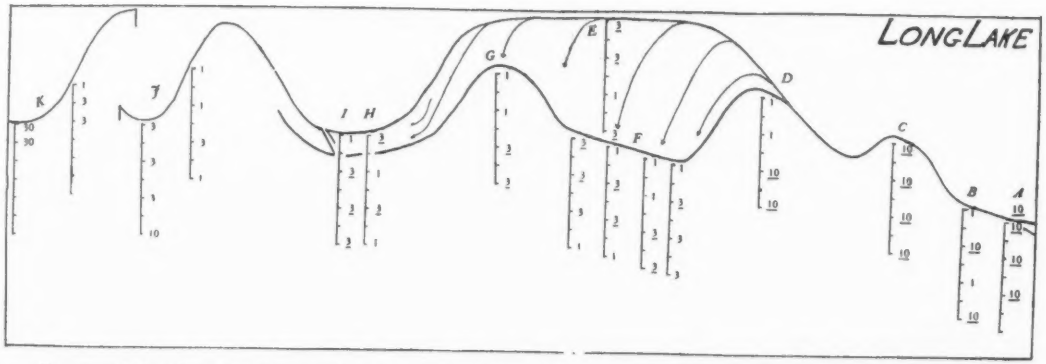

FIG. 7.—*A*, beach 20 feet from water. *B*, 100 feet from lake; SPECIES: *Calamovilfa longifolia, Ammophila arenaria, Corispermum hyssopifolium, Prunus pumila, Artemisia canadensis.* *C*, about 25 feet high; SPECIES: as at *B* but more individuals. *D*, about 50 feet high; SPECIES: *Pinus Banksiana, Calamovilfa longifolia, Ammophila arenaria, Populus deltoides, Prunus pumila, Artemisia canadensis.* *E*, moving dune with no vegetation. *F*, depression ahead of moving dune; SPECIES: *Pinus Strobus, P. Banksiana, Juniperus virginiana, Quercus alba, Q. velutina, Sassafras variifolium, Prunus virginiana, Tilia americana, Hamamelis virginiana, Cornus stolonifera, Smilax hispida, Smilacina racemosa, Polygonatum biflorum.* *G*, xerophytic unstable ridge; SPECIES: *Juniperus virginiana, Cornus stolonifera, Smilacina stellata, Rosa* sp., *Artemisia canadensis.* *H*, moist depression; SPECIES: *Pinus Banksiana, Juniperus communis, Cornus stolonifera, Maianthemum canadense, Pyrola secunda.* *I*, open; SPECIES: *Prunus pumila, Arctostaphylos uva-ursi.* *J*, about half mile from lake; SPECIES: *Populus deltoides, Quercus rubra, Q. velutina, Sassafras variifolium, Fraxinus americana, Hamamelis virginiana, Celastrus scandens, Smilacina racemosa, Aquilegia canadensis.* *K*, about a mile from lake; SPECIES: *Quercus alba, Q. rubra, Q. velutina, Sassafras variifolium, Nyssa sylvatica, Pteris aquilina, Tephrosia virginiana, Euphorbia corollata, Vaccinium pennsylvanicum, Phlox pilosa, Campanula rotundifolia, Rudbeckia hirta, Artemisia canadensis.*

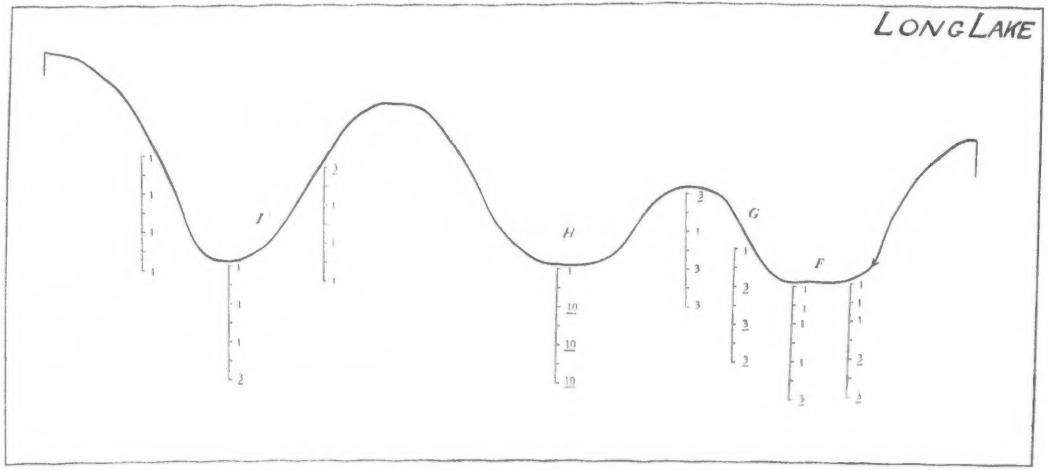

FIG. 8.—*F, I*, half mile from and parallel to *F, J* (fig. 7). *F*, moist depression; SPECIES: *Pinus Strobus, P. Banksiana, Juniperus virginiana, Maianthemum canadense, Arenaria stricta, Linnaea borealis* var. *americana, Cornus canadensis, Pyrola secunda, Vaccinium macrocarpon, Pedicularis lanceolata*. *G*, east facing slope of a 15 foot high ridge, angle 45°; SPECIES: *Pinus Stribus, P. Banksiana, Juniperus communis, J. virginiana, Rosa blanda, Cornus stolonifera, Viburnum acerifolium, Arenaria stricta, Chimaphila umbellata, Pyrola secunda*. *H*, xerophytic; SPECIES: *Pinus Banksiana, Juniperus communis, J. virginiana, Arenaria stricta, Arctostaphylos uva-ursi, Artemisia canadensis*. *I*, "pocket" in 75-foot dunes; SPECIES: *Quercus alba, Q. velutina, Sassafras variifolium, Tilia americana, Cornus florida, Hamamelis virginiana, Rhus Toxicodendron, Celastrus scandens, Lonicera Sullivantii, Aquilegia canadensis*.

canadensis and *Linnaea borealis* var. *americana* dominated it. In view of the fact that these plants grew in alkaline sands, and that decayed wood brings into play other factors besides acidity, the writer hesitates to attribute the dominance of the plants on the stump to H-ion concentration.

The data at *K* (fig. 7) are meager, but the coming in of acidity is evident. With this acidity appear *Vaccinium pennsylvanicum* and *V. vacillans*.

Mineral Springs Dunes

The highest of these dunes reach 125 feet. They are usually not more than 300–600 yards from the lake. From there on and extending back about half a mile they grade down to a more or less complex series of small ridges and depressions. Some of the older and larger dunes approach quite mesophytic conditions, with almost pure stands of *Quercus velutina*, *Q. alba*, and *Q. rubra*. Those studied, however, scarcely reach more than a late xerophytic stage, oaks dominating here, pines there, or both sharing the same habitat. About a mile from the lake the present stable frontier faces a hydromesophytic forest. This forest has developed from a bog up through the floating mat, shrub, tamarack, yellow birch-red maple-pine stages. Old tamaracks persist, but *Betula lutea*, *Acer rubrum*, *Pinus Strobus*, *P. Banksiana*, and a few *Nyssa sylvatica* dominate now. Onward through this association, 300 yards or so will bring one to where tamarack and poison sumach grade into the old floating mat of Cowles' Bog.

The Mineral Springs dunes start just as alkaline as those of Long Lake, but only a short distance from the lake they become acid. In conjunction with this acidity blueberries come in sooner than at Long Lake. No striking relationship between H-ion concentration and depth is apparent, but there are some indications of a downward diminution. The high xerophytic ridges or peaks near the lake run more nearly neutral than the slopes, while the reaction of the depressions varies with the substratum. The locality *E* (fig. 9) seems to be a tension line for *Vaccinium pennsylvanicum* and *V. vacillans*, only a few plants occurring here. There are none at *D* or *C;* from *E* to *L* they are common. *Hepatica triloba* associates with blueberries nearer the lake, but not at *K* and *L* (fig. 9).

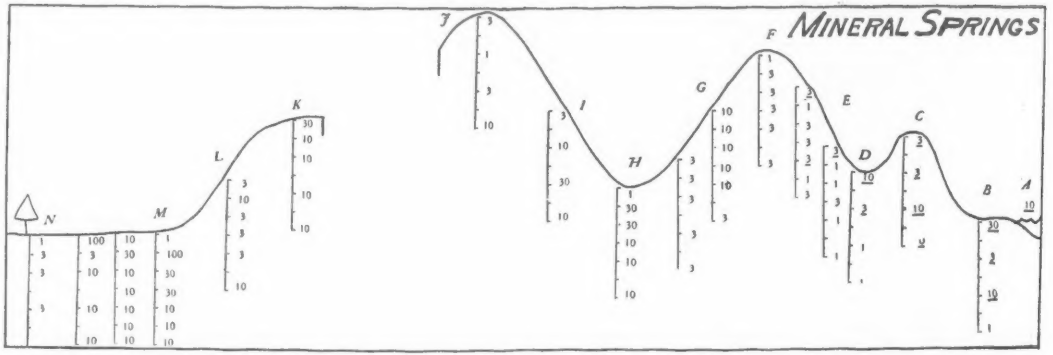

FIG. 9.—*A*, *O*, general direction southward from lake. *B*, beach. *C*, xerophytic foredune; SPECIES: *Pinus Banksiana, Rhus Toxicodendron, Vitis vulpina, Cornus stolonifera, Smilacina stellata, Monarda punctata.* *D*, just ahead of advancing foredune *C;* SPECIES: *Pinus Banksiana, Ostrya virginiana, Quercus alba, Q. velutina, Sassafras variifolium, Hamamelis virginiana, Celastrus scandens, Cornus stolonifera, Smilacina racemosa, Arabis lyrata, Monarda fistulosa.* *E*, *J*, highest dune (*J*) about 100 feet; slopes 45°; SPECIES more or less common to this series: *Pinus Strobus, P. Banksiana, Quercus alba, Q. rubra, Q. velutina, Prunus virginiana, Hamamelis virginiana, Rosa* sp., *Ceanothus americanus, Vaccinium pennsylvanicum, V. vacillans, Pteris aquilina, Hepatica triloba, Aquilegia canadensis, Aralis lyrata, Lupinus perennis, Oenothera biennis, Monarda fistulosa, Pedicularis lanceolata, Antennaria plantaginifolia.* *H*, in addition to preceding list, *Equisetum hyemale* and *Gaultheria procumbens* occur. *J*, xerophytic ridge; SPECIES: *Ceanothus americanus, Arctostaphylos uva-ursi, Vaccinium vacillans, Smilacina stellata, Oenothera biennis, Monarda punctata, Artemisia canadensis.* *K*, *M*, xerophytic frontier dune one mile from lake; height about 50 feet. *L*, south facing xerophytic slope, angle 45°; sand buff colored; SPECIES: *Arctostaphylos uva-ursi, Vaccinium pennsylvanicum, Pteris aquilina, Potentilla argentea, Lupinus perennis, Lespedeza capitata, Viola pedata, Opuntia Rafinesquii, Gaultheria procumbens, Phlox bifida.* *M*, *N*, very mature bog; soil old peat; hydromesophytic association; SPECIES: *Pinus Strobus, P. Banksiana, Larix laricina, Betula lutea, Alnus incana, Acer rubrum, Aspidium Thelypteris, Aspidium spinulosum, Osmunda regalis, O. cinnamomea, Symplocarpus foetidus, Smilacina* sp., *Maianthemum canadense, Pilea pumila, Caltha palustris, Coptis trifolia, Mitella diphylla, Podophyllum peltatum, Impatiens* sp., *Viola pallens, Pyrola secunda, Gaultheria procumbens, Mitchella repens, Linnaea borealis* var. *americana.* *N*, near floating mat; SPECIES: *Larix laricina, Alnus incana, Prunus virginiana, Ribes* sp., *Rhus Vernix, Cornus stolonifera, Vaccinium vacillans, V. corymbosum, Symplocarpus foetidus, Maianthemum canadense, Caltha palustris.* *O*, bog proper; reaction range for first six inches of mat 10–10; SPECIES: *Carex* sp., *Sarracenia purpurea, Parnassia caroliniana, Gentiana crinita.*

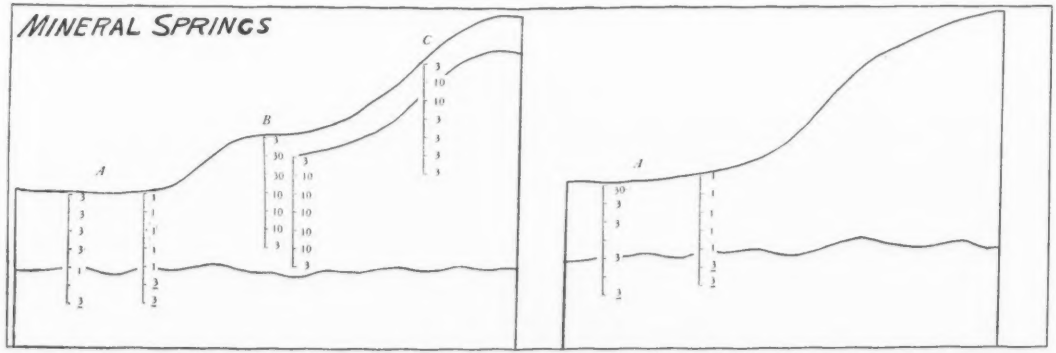

FIG. 10.—*A*, *C*, transition from another frontier dune to low hydromesophytic clay. *C*, slope of 30 foot high dune, angle 45° soil brown dune sand; SPECIES: *Quercus velutina, Sassafras variifolium, Pteris aquilina, Lupinus perennis, Viola pedata, Vaccinium pennsylvanicum, Phlox bifida.* *B*, edge of low hydromesophytic woods; soil sand high in organic matter; SPECIES: *Sassafras variifolium, Hamamelis virginiana, Osmunda regalis, Alnus incana, Vaccinium pennsylvanicum.* *C*, hydromesophytic woods proper; soil silty clay loams merging into clays about 3 feet below; SPECIES: *Populus grandidentata, P. deltoides, Betula lutea, Quercus bicolor, Ulmus americana, Fraxinus nigra, Onoclea sensibilis, Arisaema triphyllum, Symplocarpus foetidus, Trillium recurvatum, T. grandiflorum, Asarum canadense, Ranunculus abortivus, R. septentrionalis, Caltha palustris, Podophyllum peltatum, Geranium maculatum, Viola* spp., *Osmorhiza longistylis, Galium* sp.

Notwithstanding that the bog showed some local variations in reaction (*10*–10), it was evident that the floating mat was more nearly neutral than the older more or less acid hydromesophytic stage. In fig. 10 the influence of underlying clay on reaction is again shown.

Sawyer Dunes

The larger dunes near the lake at Sawyer reach a height of 300 feet. Beeches, maples, and hemlocks dominate the forest, and a remarkably luxuriant flora forms the undergrowth. In common with the other dunes studied, alkalinity is replaced by acidity in the older sands farther from the lake (figs. 11, 12). The higher acid reactions found in the mesophytic floodplain *x*, *y* (fig. 12) and in the xerophytic partially stable dune *P*, *T*, *S* (fig. 12) diminish below.

The sandy floodplain has a very irregular H-ion concentration, varying from 1 to 300. Alluvial material washed in from the upstream moraine probably is one of the factors operating toward neutrality. Decaying logs, organic matter, together with a high water table, on the other hand, increase acidity locally. Most of the spring flowering plants and ferns found in the mesophytic dunes grow equally well in these soils, whether acid or neutral. In fact the writer has data, to be published later, showing that most of the spring flowers and ferns mentioned in this paper grow in soils ranging from a specific alkalinity of *3* or *10* to a specific acidity of 100 or 300. In contrast with Long Lake and Mineral Springs, *Vaccinium pennsylvanicum*, *V. vacillans*, or *Gaylussacia baccata* do not come in with acidity here.

Baroda Bog

Nestled in the moraine, about 7 miles from the Sawyer dunes, and 2 miles from Baroda, Michigan, lies a small lake with a bog on its eastern fringe. The bog merges from a floating mat to black friable soil which supports a typically mesophytic vegetation. It seems that the younger mat (and older sections also if low) are kept alkaline or neutral by the alkaline lake water. The higher forested portion is not so accessible to the water, and therefore influenced less. In any event, we have here evidence of an alkaline mat becoming neutral or slightly acid as a forest develops on it.

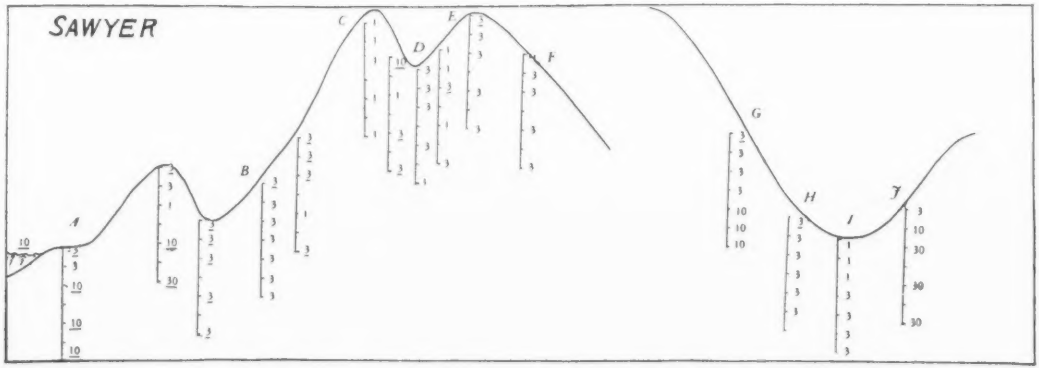

FIG. 11.—*A*, *J*, highest dunes about 300 feet; slopes about 45°; excepting *A* and *B*, forest dominated by *Tsuga canadensis*, *Fagus grandifolia*, and *Acer saccharum*, but following not uncommon: *Juglans cinerea*, *Ostrya virginiana*, *Carpinus caroliniana*, *Quercus alba*, *Q. rubra*, *Ulmus americana*, *Sassafras variifolium*, *Hamamelis virginiana*, *Prunus serotina*, *Ptelea trifoliata*, *Tilia americana*, *Fraxinus americana*, *Sambucus canadensis*. Undergrowth: *B*, almost a pure stand of *Taxus canadensis*; *C*, *J*, herbaceous species, *Adiantum pedatum*, *Polystichum acrostichoides*, *Aspidium marginale*, *A. spinulosum*, *Uvularia grandiflora*, *Erythronium americanum*, *Smilacina racemosa*, *Maianthemum canadense*, *Polygonatum biflorum*, *Trillium recurvatum*, *T. grandiflorum*, *Claytonia virginica*, *Hepatica triloba*, *Anemone quinquefolia*. *Isopyrum biternatum*, *Aquilegia canadensis*, *Podophyllum peltatum*, *Sanguinaria canadensis*, *Dicentra Cucullaria*, *Dentaria laciniata*, *Mitella diphylla*, *Viola* spp., *Osmorhiza longistylis*, *Hydrophyllum* sp., *Mitchella repens*.

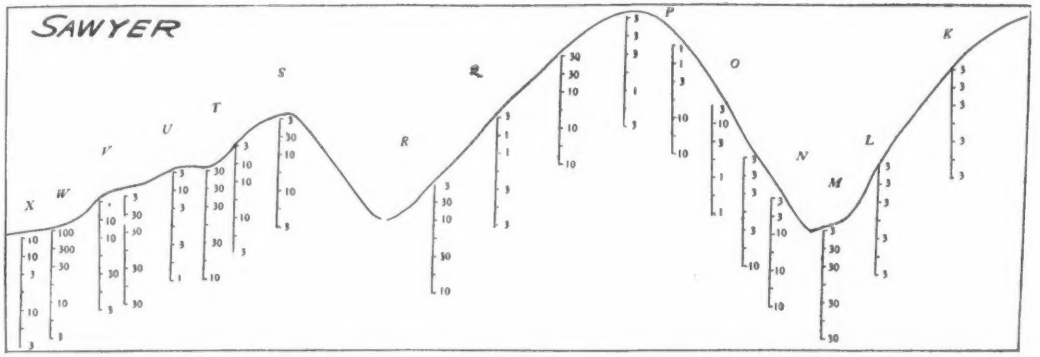

FIG. 12.—*K*, *X*, approximately parallel to *A*, *J* (fig. 11), but beginning about one-fourth mile from lake and ending half mile farther inland in sandy floodplain of a creek that winds through dunes to lake. *K*, *R*, rich mesophytic association similar to that of *C*, *J* (fig. 11). *S*, *X*, series running from xerophytic unstable dune to hydromesophytic sandy floodplain at *X*, *W*. *S*, xerophytic unstable dune about one-fourth mile from *R;* height about 50 feet; soil sand; SPECIES: *Prunus virginiana, Rumex acetosella*. *T*, *U*, xerophytic partially stable slope; soil sand; SPECIES: *Carya cordiformis, Prunus virginiana, Rhus typhina, Rumex acetocella, Oenothera biennis, Monarda fistulosa, Verbascum thapsus*. *V*, becoming mesophytic. *W*, *X*, hydromesophytic floodplain; soils sands with alluvium and high organic content; forest same as at mesophytic dunes, with addition of *Betula lutea* and *Platanus occidentalis;* HERBACEOUS SPECIES: *Adiantum pedatum, Polystichum acrostichoides, Aspidium marginale, A. spinulosum, Onoclea sensibilis, Osmunda regalis, O. cinnamomea, Uvularia grandiflora, Erythronium americanum, Smilacina racemosa, Maianthemum canadense, Polygonatum biflorum, Trillium recurvatum, T. grandiflorum, Ranunculus septentrionalis, Hepatica triloba, Anemone quinquefolia, Caltha palustris, Podophyllum peltatum, Cardamine* sp., *Mitella diphylla, Impatiens* sp., *Viola pallens, V. scabriuscula, Erigenia bulbosa, Osmorhiza longistylis, Pyrola secunda, Mitchella repens, Linnaea borealis* var. *americana*.

The writer searched for locally acid patches, but found none except a few hummocks at *E* (fig. 13), where *Sphagnum* and *Drosera rotundifolia* were growing intermingled. Here the specific acidity was 30, but extended only a few inches down. In one case *Parnassia*

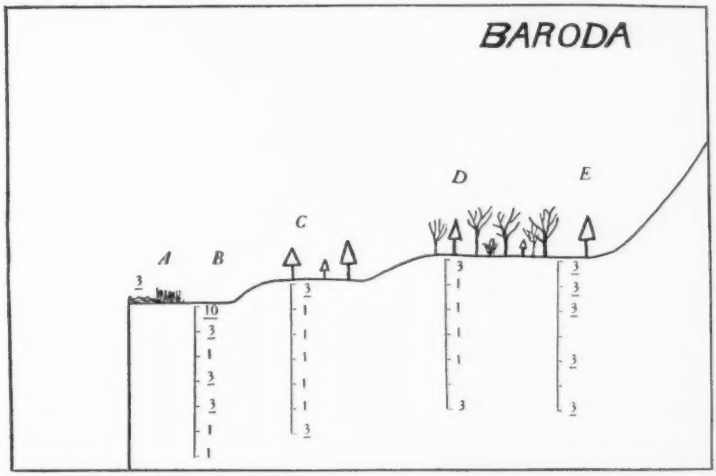

FIG. 13.—*A*, thin mat; SPECIES: *Typha latifolia*, *Scirpus* sp., *Carex* spp. *B*, mat 3 feet thick or more; SPECIES: *Aspidium thelypteris*, *Typha latifolia*, *Hypoxis hirsuta*, *Sisyrinchium angustifolium*, *Cypripedium hirsutum*, *Nymphaea advena*, *Caltha palustris*, *Sarracenia purpurea*, *Parnassia caroliniana*, *Lysimachia thyrsiflora*. *C*, about 6 inches of black organic soil, peat below; SPECIES: *Larix laricina*, *Ulmus fulva*, *Acer saccharum*, *A. rubrum*, *Fraxinus americana*, *Hamamelis virginiana*, *Pscdera quinquefolia*, *Cornus alternifolia*, *Sambucus canadensis*, *Aspidium thelypteris*, *A. cristatum*, *Arisaema triphyllum*, *Symplocarpus foetidus*, *Laportea canadensis*, *Pilea pumila*, *Phytolacca decandra*, *Ranunculus septentrionalis*, *Mitella diphylla*. *D*, mat higher; soil black friable above and peat below; SPECIES: fewer tamaracks but all species of *C* are here, plus *Aspidium spinulosum*, *Maianthemum canadense*, *Trillium recurvatum*, *Ranunculus abortivus*. *E*, open and lower old mat; *Larix laricina*, one *Platanus occidentalis*, *Sphagnum* (few mats), *Aspidium thelypteris*, *Typha latifolia*, *Caltha palustris*, *Drosera rotundifolia* (few plants), *Parnassia caroliniana*.

caroliniana, with its roots in a substratum of specific alkalinity 10, sent its stem up through a mat of *Sphagnum* of specific acidity 10. Elsewhere the writer has sometimes noted that the acidity of *Sphagnum* beds is not far reaching, either vertically downward or laterally away from the mat. It has also been observed at times

that the acidity under *Osmunda regalis* may be much higher than 3 feet away from the plant. Such very local acidity seems to be an incidental product of these plants.

Chesterton Bog

Near Chesterton, Indiana, a bog has developed in an oxbow of the Calumet River. Similar to the Baroda bog, the upper foot or so of the peat has decomposed into a very black friable soil; below the raw peat is present. The site was studied late in the winter, so that a complete list of the plants could not be obtained. The dying tamaracks, however, and the invasion of mesophytic forest trees indicate the very old age of this bog.

Just how generally acid, if at all, these bogs have been the writer does not know. In any event, they show a general neutrality or alkalinity at a stage which is well toward mesophytism. Alkaline or neutral sections were the rule in the Baroda bog, even where pitcher plants and tamarack are still thriving, but when by decomposition the peats become a black friable soil, mesophytes establish themselves. It seems that the reactions per se of these soils have no influence on the coming in of these mesophytes, for many of them tolerate a range of *10–300* in other types of habitats.

The Thornton Forest Preserve was selected as the site for some observations of the effect of seasonal phenomena on the H- ion concentration. The stations *A*, *B*, *C*, *C*^{1}, *I*, *J*, *K*, *L*, *R*, and *S* of figs. 1, 2, and 3 were visited a number of times during 1921 and 1922. Excepting the first, borings were always made about 3 feet from any previous one. The data are given in table I, the stations being labelled by capital letters. Although at least five kinds of soils and habitats are included in these studies, one sees no decided change in reaction. Stations *C*, *C*^{1}, *I*, *K*, *L*, and *S* indicate a diminution of acidity for the winter months, but after thawing rain and drouth periods no fluctuations were observed. The decreases indicated by these stations during the winter months may be real or possibly due to local variations. To determine this one would have to study the habitats more intensively.

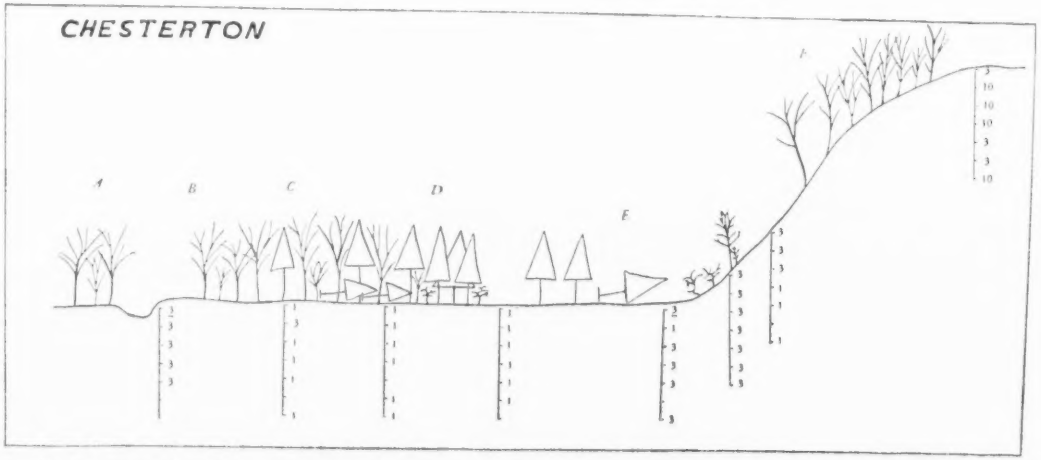

FIG. 14.—*A*, *B*, floodplain; soil alluvial clay; SPECIES: *Carya ovata, Fagus grandifolia, Quercus alba, Ulmus americana, Tilia americana, Fraxinus americana, Carpinus caroliniana, Cornus stolonifera*. *C*, *E*, soil of peat origin; SPECIES: *Larix laricina* (no seedlings); *Populus deltoides, Alnus incana, Quercus alba, Fraxinus americana, Rhus vernix, Cornus stolonifera, Sambucus canadensis, Conocephalus conicum, Symplocarpus foetidus*. *E*, *F*, gravelly morainic ridge about 25 feet high; SPECIES: *Rhus vernix* and *Sassafras variifolium* at bottom, and *Fagus grandifolia, Quercus alba, Q. rubra*, and *Ulmus americana* on slope and top.

TABLE I

	A					C					C′				
After heavy rain 9-12-21¶	3	3	3	3	10*	3	3	3	3	10	10	10	10	10	10
After 2 weeks almost continuous rains 9-21-21	3	1	1	1*	.....	3	3	10	1	3	3	3	10	1	3
After 6 weeks more or less cool weather 11-20-21	1	1*	.....	.....	.....	3	10	10	10	3	3	10	10	10	10
Frost 4 in., 7 in. snow 12-28-21	1*	1*	1	1	.....	3	10	10	10	1	10	10	10	10	3
Frost about 6 in. 3-6-22	1*	1	1	1	1	3	10	10	10	1	10	10	10	3	10
Frost gone after 18 hours rain 3-26-22	1*	1	1	1	1	3	10	10	10	1	3	10	30	3	10
Wet spring weather 5-13-22	1	1	1*	.....	.....	10	30	30	100	10	3	10	30	1	3
After 40 days drouth 7-9-22	1	1	3	1	1	3	30	10	10	3	3	100	30	3	3
After heavy rain 9-12-21	300	100	300	100	30	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
After 2 weeks almost continuous rains 9-21-21	300	100	300	100*	3	3	3	3	3	3	30	30	10	10	3
After 6 weeks more or less cool weather 11-20-21	100	100	100*	100	1	3	3	3	3*	.....	30	30	10	10	3
Frost 4 in., 7 in. snow 12-28-21	100*	100*	100	100	30	10*	10	3	1	.....	30	30	30	30	10
Frost about 6 in. 3-6-22	300*	300*	300	300	30	10*	10	3	3	3	100	100	100	30	10
Frost gone after 18 hours rain 3-26-22	100*	300	300	300	30	3*	3	10	3	10	100	100	100	10	10
Wet spring weather 5-13-22	300*	300	300	300	3	10	3	1*	3	3	.....	.....	.....	.....	.....
After 40 days drouth 7-9-22	300	300	300	300	10	10	10	10	10	1	300	300	100	10	10
After heavy rain 9-12-21	.....	.....	.....	.....	.....	100	30	10	10	10	100	100	100	100	30
After 2 weeks almost continuous rains 9-21-21	.....	.....	.....	.....	.....	10	10	10	10	10	100	100	100	100	100
After 6 weeks more or less cool weather 11-20-21	.....	.....	.....	.....	.....	3	10	10	10	3	100	100	100*	100	100
Frost 4 in., 7 in. snow 12-28-21	.....	.....	.....	.....	.....	10	10	10	10	3	100	30	100*	100	100
Frost about 6 in. 3-6-22	3	30	30	10	10	3	30	10	10	10	100	100	100*	30	100
Frost gone after 18 hours rain 3-26-22	3	10	30	10	10	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Wet spring weather 5-13-22	10	30	30	10	10	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
After 40 days drouth 7-9-22	3	30	30	10	10	3	30	10	10	10	300	300	300	300	300
After heavy rain 9-12-21	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
After 2 weeks almost continuous rains 9-21-21	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
After 6 weeks more or less cool weather 11-20-21	3	10	10	10	10	3	10	10	10	10	100	100	100	100	100
Frost 4 in., 7 in. snow 12-28-21	10	10	3	1	1	10	10	10	10	3	100	30	100*	100	100
Frost about 6 in. 3-6-22	3	30	30	10	10	3	30	10	10	10	100	100	100*	30	100
Frost gone after 18 hours rain 3-26-22	3	10	30	10	10	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Wet spring weather 5-13-22	10	30	30	10	10	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
After 40 days drouth 7-9-22	3	30	30	10	10	3	30	10	10	10	300	300	300	300	300
After heavy rain 9-12-21	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
After 2 weeks almost continuous rains 9-21-21	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
After 6 weeks more or less cool weather 11-20-21	3	10	10	10	10	3	10	10	10	10	100	100	100*	100	100
Frost 4 in., 7 in. snow 12-28-21	10	10	3	1	1	10	10	10	10	3	100	30	100*	100	100
Frost about 6 in. 3-6-22	3	30	30	10	10	3	30	10	10	10	100	100	100*	30	100
Frost gone after 18 hours rain 3-26-22	3	10	30	10	10	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Wet spring weather 5-13-22	10	30	30	10	10	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
After 40 days drouth 7-9-22	3	30	30	10	10	3	30	10	10	10	300	300	300	300	300
After heavy rain 9-12-21	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
After 2 weeks almost continuous rains 9-21-21	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
After 6 weeks more or less cool weather 11-20-21	3	10	10	10	10	3	10	10	10	10	100	100	100

Summary

1. Loams, silts, or clays of the upland or slopes, whether of morainic, dolomitic, or loess origin, were nearly always found to be more acid than the immediate alluvial floodplain soils. The drainage waters were always alkaline. The results of selective leaching of bases are thus nicely emphasized.

2. The dunes nearest the lake are composed of alkaline sands. Farther from the shore where dunes are older, alkalinity is gradually replaced by acidity. Selective leaching seems again to be operative.

3. In the alkaline dunes the peaks and depressions showed no appreciable difference in acidity. When acidity becomes established, the slopes and depressions are more acid than the peaks. The explanation lies perhaps in the differences in moisture and organic content, aeration, leaching, etc.

4. The flat, poorly drained sand soils of Thornton were found to be higher and more consistently acid than any of the three bogs mentioned in this paper. A high water table and consequent poor aeration, together with a poverty of bases, are some of the causative agents.

5. The floating mat stages (excepting locally sphagnum beds, etc.) of bogs and very old soils of bog peat origin gave circumneutral reactions. Only in the hydromesophytic portion of Cowles' bog were acid reactions typical. Even here the acidity was often slight.

6. Soils of high acidity usually showed a diminution below, in some cases becoming actually alkaline at a depth of 3 feet. The underlying strata determine the reactions below.

7. Heavy rainfall, drouth periods, freezing, and thawing caused no important fluctuations in H-ion concentrations in the stations studied.

8. Nearly all of the spring flowers, many ferns, and some hitherto so-called acid soil plants were found growing in soils ranging from definite alkalinity to high acidity. H-ion per se, therefore, is not the main factor in determining the distribution of the species considered.

9. Acid clays or silts and acid sands were characterized by two decidedly different plant associations. Again, certain sands,

whether alkaline or acid, had in common many plants not found in acid or alkaline silty or clayey soils.

I am indebted to Dr. H. C. COWLES and Dr. GEO. D. FULLER for encouragement, suggestions, and aid during the progress of the work; and to Dr. EDGAR T. WHERRY for suggesting methods of attack. Thanks are due to FRANK THONE and DELZIE D. DEMAREE for help in collecting samples at times, and to ROBERT B. DUSTMAN for aid in classifying some of the soils.

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ROOT HAIRS AND SECONDARY THICKENING IN THE COMPOSITAE[1]

EDITH S. WHITAKER[2]

(WITH PLATES I–V AND SIX FIGURES)

Root hairs appear a short distance behind the root tip where the cells are dividing, and as a rule persist for a comparatively short time. As the hairs die off new ones are formed nearer the growing point, giving rise to what has been termed "the migration of root hair zones" (1). Root hairs are intimately connected with soil particles, and are the chief means through which water and mineral salts are taken from the soil into the plant. Water and air roots present a different situation with respect to absorption which is not of primary concern in this discussion. So far as I have been able to discover, the fact that root hairs are ever more than ephemeral structures has not been emphasized in the standard textbooks of plant morphology or of plant anatomy. Neither have I been able to find in such works statements correlating in a definite way the presence of root hairs with the primary organization of the vascular tissues of the radial cylinder. Most of the illustrations depicting the radical organization of the xylem and phloem elements in young roots show hairs present at the outer edge. Doubtless the fact that root hairs have so generally been assumed to be transient structures is responsible for the lack of more definite information concerning the two.

It has recently been noted (3) that in certain herbaceous forms there is what may properly be called the herbaceous type of root, which differs from the usual woody root in that it is characterized externally by persistent root hairs in most instances, and by the absence, internally, of any considerable amount of secondary thickening. In certain genera root hairs have been noticed to per-

[1] Contribution from the Laboratories of Plant Morphology of Harvard University.

[2] Alice Freeman Palmer Traveling Fellow of Wellesley College, 1920–1921.

sist for several seasons, particularly in the case of the herbaceous biennials and perennials.[1]

Since it has recently been noted in many instances that roots remain hirsute until the end of the season, or, in the case of certain herbaceous perennials, for more than one season, it was proposed to investigate several genera of the Compositae, a family of recognized herbaceous character, to see whether they might be of general occurrence, or merely a unique habit of some species. In making this investigation, seven genera of the Tubuliflorae were studied: *Aster* (6 species), *Solidago* (7 species), *Eupatorium* (6 species), *Vernonia* (3 species), *Helianthus* (1 species), *Dahlia* (2 species), and *Chrysanthemum* (2 species). Most of the roots were collected in or around Cambridge from late September to mid-November, that is, well after the period of growth and greatest absorption had passed. Plants of the salt marsh goldenrod and of *Eupatorium maculatum* were brought into the laboratory, the old roots cut off, and the plants put into a rich, moist humus, to see what might be the effect of a change of environment on the production of root hairs. Seedlings of some species were available for investigation, but unfortunately not in all instances. The roots were preserved in chrom-acetic acid, imbedded in parlodion, stained with iron-haematoxylin, and mounted in Canada balsam.

Before 1883 comparatively little work had been done on root hairs. SACHS' *Lehrbuch* (**8**), which was translated into English in 1875, has only a very brief account of them. In 1883, SCHWARZ (**9**) presented the fullest and most complete study of root hairs that had been published up to that time. He pointed out the direct advantage to be gained from the point of view of increasing the amount of absorbing surface:

> Bestimmung und Zweck der Wurzelhaare . . . . ist ja doch von vornherein klar, dass durch die Haare die Wurzeloberfläche bedeutend vergrössert und dass durch den innigen Contact der Haare mit Bodentheilchen die Stoffaufnahme ausserordentlich erleichtert wird. . . . . Bei *Zea* war die Oberfläche der behaarten Wurzeln $5\frac{1}{2}$ mal grösser als bei nackten.

[1] When this investigation was nearly completed, an article appeared by MCDOUGALL (**5**), in which he reported the presence for several seasons of root hairs in *Gleditsia triacanthos*, *Cercis canadensis*, and *Gymnocladus dioica*. The production of root hairs in these genera, as well as MCDOUGALL's conclusions, will be considered later in this paper.

From his researches, SCHWARZ concluded that the production of root hairs was closely related to, or dependent on, the moisture content of the medium in which the plants were grown. He does not correlate root hair production with growth intensity, but he does assign other causes of hair production than moisture alone, such causes being the amount of available oxygen, nourishment, and pressure or resistance which causes "Nutationen" or "Kinking." Since this work of SCHWARZ on root hairs, various physiological interpretations have been evoked to elucidate their formation. A few of these that have either an historical interest or some bearing on the problem at hand will be mentioned briefly.

KERNER (4) correlates the position of the foliage leaves to the absorbing roots. He points out that when the leaves are so arranged that the water is shed from the ends of the branches and does not run down the trunk or stem, the region of absorbing roots is to be found at the periphery of the circle which marks the diameter of the branches. Plants whose leaves are vertically disposed have a centripetal method of water conduction, and correspondingly have tap roots, or roots that penetrate the ground more or less vertically and near the basal region. PFEFFER (7) notes that roots growing either in a saturated atmosphere or in a moderately dry soil produce the largest number of root hairs. STRASBURGER (13) notes that "the older parts of roots, even in plants which persist for many years, take no part in the process of absorption. . . . . Even in young roots the absorption seems principally confined to the region covered with root hairs, or in case no hairs are developed, to a corresponding zone of the epidermis." He makes no mention of the persistence of root hairs except for a comparatively short period of time.

An extensive piece of work on root hairs was published by Miss SNOW (10) in 1905. Her last conclusion, for which she appears to adduce no supporting evidence in the text, is of interest. She states that "the activity of the epidermis may be in inverse proportion to the activity of the central cylinder, lateral roots often appearing when hairs are suppressed, and vice versa." If she had stated that secondary growth appeared when root hairs were suppressed, she would have come very near to the facts of the case as illustrated by the genera of Compositae here described.

In connection with the discussion of turgidity in relation to growth, PALLADIN (6) makes the following statement about thick-walled root hairs.

> WORTMANN found, in experiments with *Lepidium sativum*, that root hairs are very long and thin when grown in water, while they remain short and their cell walls are much thickened when they are grown in sugar solutions. The cellulose that produced the increased expanse of cell wall in the first case produced thickening in the second case. The same thing occurs when the water supply is not sufficient for the usual growth of the plant, small cells with thick walls being produced in this case also.

In the same connection, a statement by COULTER, BARNES, and COWLES (1) is of interest:

> The root hairs of some xerophytes have rigid, lignified walls; for example in *Pinus edulis* they are stiff and brown. In some succulent xerophytes (as *Opuntia*) hairs occur to the extreme root tip.

It will be seen that explanations offered for the appearance of root hairs are largely physiological in character, and that the production and continued existence of root hairs have not yet been correlated in a specific way with the internal organization of the root.

As is well known, in roots the characteristic organization of the vascular elements, as distinguished from typical stem topography, is radial; that is, the xylem and phloem, instead of facing each other, occur in alternating radii. The woody cylinder is usually a protostele, and the development of the wood is centripetal, the first formed elements being at the outer edge of the stele, while the later formed metaxylem cells occupy the center. The vascular cylinder in roots is always bounded externally by a circle of cells with peculiar suberized walls, the endodermis. In young roots there is a large cortex made up of thin-walled storage cells, and at the outer edge of the cortex, a piliferous or root hair-forming layer. The root hairs themselves are merely elongations of the superficial cells at right angles to the axis of the root. Inside the root hair-bearing layer there is often an exodermis, consisting of a single row of cells (sometimes two or three rows) with walls thicker than is characteristic of most of the cortical cells. The exodermis, unlike the endodermis, which is a very old structure, is probably a fairly

new and rather inconstant feature of root organization. It is mentioned here because it occurs so constantly in the genera under discussion.

The primary stele is laid down by the primary meristem; that is, the cells are without specially regular linear disposition. The cell walls of the primary tracheids are usually, but not always, characteristically thickened in a spiral and not uniformly throughout. Growth in thickness, up to the time that growth in length ceases, is due to the enlargement of the cells themselves. This is known as primary thickening. When growth in length has ceased, growth in width begins, resulting in the collateral arrangement of the conducting elements characteristic of most woody stems, and of roots of plants which grow for many years, as pines, birches, oaks, etc. Roots with secondary thickening also occur in herbaceous perennials and in some annuals. The secondary tracheids, in addition to being radially disposed, are generally thickened uniformly, and have thin places on their cell walls known as pits. Specialized cells, such as vessels, storage cells, fibers, complete the organization of the woody cylinder that is thickened in this secondary fashion; that is, secondary thickening is usually accompanied by a high differentiation of elements and a marked division of labor. The cortex appears relatively smaller, and a corky layer, initiated by a special cambium, appears at the outer edge of the root. The beginning of the periderm layer marks the end of absorption in the root, and is begun only after the root hairs have ceased to function.

STEVENS (12) explains the radial arrangement of the primary tissues as follows:

> The purpose of the radial arrangement of the primary xylem and phloem of roots appears to be to allow the water absorbed by the root hairs to pass into the xylem highways without first traversing the food highways in the phloem The changes brought about by secondary thickening would not interfere with this purpose because they occur in the older parts of the root where root hairs have already died away.

This seems to be a reasonable explanation, and one that is in accord with the facts of the case as presented by the roots themselves.

A similar interpretation is brought forward in a recent article by JEFFREY and TORREY (3):

> In the root the most obvious interpretation of the absence of secondary growth is the unfavorable effect that a jacket of secondary elements would have on the case of penetration of the water absorbed by the root hairs into the water-conducting tissues of the central cylinder.

In stems it is generally recognized that the herbaceous habit is marked by a reduction in woody tissues. There is a corresponding conversion of woody segments opposed to the outgoing leaf traces into broad bands of radially arranged storage tissue. In extreme herbs only flanking parenchyma appears, due to the thinning of the cylinder. There is a marked decrease in cambial activity, especially in relation to the foliar traces. In roots the herbaceous habit is likewise accompanied by a reduction of secondary tissues, a decrease in cambial activity, and in many instances by the persistence for a considerable space of time of the root hairs. The Compositae offer a good opportunity for a comparative study of both woody and herbaceous types of roots and stems. One might expect to find a correspondence in degree of herbaceousness in stem and root; this, however, is not always or necessarily the case, as the situation in root and stem of a given species with respect to secondary activity is not always the same.

Aster

Among the Compositae, *Aster* in many respects affords the best examples of woody and herbaceous types of roots. Six species of *Aster* were studied: *A. umbellatus*, *A. tataricus*, *A. Shortii*, *A. ptarmacoides*, *A. novae-angliae*, and *A. puniceus*. Roots of the seedlings of *A. umbellatus* and *A. puniceus* were available. The material, with the exception of the roots of *A. puniceus* and certain roots of the hoary aster which grew in a swamp in Cape Breton, was collected in and around Cambridge, including the Harvard Botanic Garden, late in October 1920.

A. umbellatus, the hoary aster with the few white rays which is rather common to the northward in moist thickets, has very long roots of medium size, and fairly large secondary roots which are comparatively few in number. The roots come off mostly from

the base of the main aerial stem, there being very few on the long rootstock. Roots of this species were conspicuously hirsute, the hairs being fairly well distributed from the proximal to the distal end of the root. The secondary roots likewise were well provided with root hairs. The young or seedling plants showed a similar distribution of root hairs, especially at the proximal end, although the development of the roots, both in size and number, was of course considerably less. The specimens taken from a peat swamp were also persistently and conspicuously hirsute.

Fig. 1. is a transverse section through a root of *A. umbellatus* at the end of its second year of growth. Under the comparatively low degree of magnification the seven points of the primary xylem can easily be distinguished. That there is a very slight development of secondary wood outside the primary xylem is evident. The alternating clusters of phloem are difficult to detect under this degree of magnification, but they are included within the arcs formed by the different groups of secondary elements. Just outside the endodermis are seven well developed oil canals, which, it is to be noted, alternate with the seven points of the primary xylem; that is to say, they are arranged in the same radii as are the phloem aggregations. The presence of oil or resin canals is a diagnostic feature of the roots of the Tubuliflorae (11). The cortex is conspicuously wide, and in this particular specimen has been broken in several places, due either to growth tension, or more probably to frost action. The outer cortical cells in this specimen were infected with a fungus of some sort, but in general the roots were free from fungal infection. Root hairs are easily distinguished at the outer edge. The cell walls are not appreciably thickened, a fact which would seem to favor the assumption that the root hairs, even at the end of the second year of growth, are still functional. This assumption is further strengthened by the slight amount of secondary growth.

Fig. 2 is a transverse section through the root of the same species of *Aster*, made at the end of the first season of growth. Here the stellate condition of the primary wood is quite apparent, and the alternating lays of phloem can easily be seen under the six (five in this instance, the canal on the upper left in this section being abortive)

oil canals. The cortex is wide in diameter, and it is to be noted that just inside the piliferous layer is a row (usually one, sometimes more) of cells with thicker walls, which give support to the root, the exodermis. Roots hairs are most conspicuous, and their thin-walled character will be noted by referring to fig. 5, which shows some of them magnified 500 times. The purely primary character of the central cylinder will readily be conceded.

Fig. 3 shows the organization of a root of *A. umbellatus* which grew in a peat bog. This particular specimen came from Cape Breton, but roots of specimens ranging from Nova Scotia to Massachusetts grown under similar conditions presented similar organization. At the end of the season the woody cylinder is conspicuously without secondary growth, although there is a trace of cambial activity. This is more evident in the high power magnification of the vascular cylinder shown in fig. 4. The oil canals, which are characteristic of this species, are here imperfectly developed. That the root is hairy is evident, the root hairs being very long and as characteristically thin-walled as are those of the same species which grew in garden soil.

Fig. 6 represents a transverse section of a mature absorbing root of *A. tataricus*, which is likewise permanently hairy. The primary wood is hexagonal, and the root hairs of this extremely herbaceous species are so fine that many of them were sloughed off in the process of imbedding. A few that had survived the process may be noted at the right in the illustration. In contrast, the mechanical roots have a well developed cylinder of secondary wood, a much reduced cortex, and no root hairs. The absorbing roots are most densely hairy at the proximal end, and are often entirely without hairs distally. The proximal distribution of hairs is characteristic of many of the permanently herbaceous roots.

Turning now from a persistently hairy type of root, as represented by *A. umbellatus*, the situation obtaining in a more woody type of root, such as *A. Shortii*, may be considered. Fig. 7 represents an old root of this species in transverse section, and the large amount of secondary growth is most conspicuous. The star-shaped primary xylem aggregation in the center can be noted clearly, and alternating with its five points, although well out toward the

periphery of the secondary cylinder, the semi-oval groups of primary phloem can be seen. The endodermis is still a prominent feature of the section, and the reduction in size of the cortex is noticeable. It will also be noted that oil canals are absent, as is true both in old and younger roots, or they are at most only vestigial. Correlated with the large amount of secondary growth is the disappearance at the outer margin of root hairs. No cork layer is present, however, although the outer cells of the cortex have become considerably thickened. The young roots of *A. Shortii* show both well developed root hairs and a marked deficiency of secondary growth. This situation is made evident in fig. 8, which is of a transverse section of a younger root of the same species. Here the wide cortex is a distinguishing feature. The root hairs are thin-walled, as would be expected in young roots. The root hairs here figured are several weeks old, and therefore are not to be classed as purely ephemeral structures.

Another species in which the mature roots are woody, while the younger roots exhibit the herbaceous type of organization, is *Aster novae-angliae*, a showy, handsome species with violet-purple rays and auriculate-clasping leaves, found usually in sweet soils. The old roots, like those of *A. Shortii*, are conspicuously woody, although the extent of woodiness is not quite so great as in the latter. Fig. 9, which represents the mature root of *A. novae-angliae* in cross-section, shows no root hairs, although they often do persist in a shrivelled state long after they have obviously ceased to function. Fig. 10 is a younger root of the same species. Here the five-angled nature of the pith is more evident than in fig. 9, and the amount of secondary wood is relatively small. The cortex is larger, and there are no oil canals either in the young or old roots of the species, a condition more or less general in species that later become woody. The exodermis just inside the piliferous layer is quite conspicuous in this figure. Very long and numerous root hairs are to be noted at the edge of the root.

A species resembling *A. novae-angliae* in its auriculate leaves and its bluish flowers is *A. puniceus*, which is found in swamps and low thickets. Seedlings of *A. puniceus* were available for comparative study with the older roots. The mature roots were conspicuously

smooth throughout, but the roots of the seedlings were abundantly hirsute, especially proximally. The internal structure of the mature and seedling roots is figured in the following illustrations. Fig. 11 represents a cross-section of a mature root of *A. puniceus*. The secondary wood is obviously poorly developed, and the five-angled primary elements stand out markedly as a consequence. Outside the endodermis, and in the same radii with the primary phloem elements, the five oleo-resin canals may be noted. The cortex, which is wide in extent is loose in texture, and is abundantly provided with air spaces. It will be seen that there are no root hairs, the absorbing function having probably been assumed by the superficial cells. That there are root hairs and a well developed piliferous layer in the young or seedling root is evident in fig. 12, a transverse section through a young root of the same species. The root hairs are numerous, long, and thin-walled. Air spaces are just beginning to appear in the cortex. The relations with respect to cortical air spaces between seedlings and mature root in this species may be compared with the situation obtaining in certain vines, the bittersweet for example, which is at first woody, but which later becomes herbaceous. Just outside the endodermis are the five oil reservoirs that alternate with the five points of the primary xylem. The five groups of primary phloem are easily distinguished as dark areas just outside the five secondary bundles. It is an interesting and significant fact that here are two cylinders, one representing a mature root, the other a young root of the same species, and that while neither exhibits marked development of secondary wood, the one is entirely glabrous, the other densely hirsute. The situation obtaining in the woody organization of the mature root of *A. puniceus* is characteristic of the roots of the most advanced herbs. This specialization of root structure reaches its height in the monocotyledonous roots on the one hand, and the *Ranunculus* type on the other hand, in which the vascular organization is permanently primary, but which is without root hairs even in the seedling condition.

The roots of *A. puniceus* were collected in the same swamp as were the roots of *A. umbellatus* shown in fig. 3. The former species has permanently smooth roots, the latter permanently hairy

roots, while both are hirsute in the seedling stage. In many cases the roots of the two species were found intertwined, so that the habitat and conditions of existence of the two are the same. It would be difficult in this case to explain the production or the non-production of root hairs on a purely physiological basis.

A. ptarmacoides, which is not figured here, was found to be similar in organization to *A. Shortii* and *A. novae-angliae*. In the young condition the woody cylinder is composed of primary elements, the protoxylem clusters being arranged in four points. The cortex is wide and without oil canals. Root hairs are well developed. In the mature root, on the contrary, the primary elements are obscured by the extensive secondary growth, the cortex is appreciably diminished in extent, and the periphery is without root hairs. The roots that had hairs on them at all possessed them at the proximal ends, that is, near the place where the root came off the stem. In contrast, the distal parts of the roots were generally smooth, a situation which occurs often in herbaceous roots, and which may be designated as *basipilose*. Roots without any hairs in the mature stage may be referred to as *apilose*, and those with root hairs behind the growing point only as *punctipilose*.

Solidago

The distribution of root hairs was investigated in the following species: *Solidago tenuifolia*, *S. canadensis*, *S. serotina*, *S. rugosa*, *S. patula*, *S. sempervirens*, and *S. graminifolia*. Fig. 13 is a transverse section of a mature root of *S. tenuifolia*. Obviously the woody cylinder is composed almost entirely of secondary elements; in fact, it is difficult to distinguish the four protoxylem points. The four primary phloem groups, however, can readily be noted at the edge of the endodermal sheath. The cortex is relatively thin. The difficulty of distinguishing clearly the protoxylem groups in roots is explained by the fact that growing roots are often subjected to considerable pressure, which results in the crowding of the primary elements by the more numerous and more highly specialized secondary tissues. In longitudinal section it is likewise often hard to distinguish the primary tracheids from the secondary ones, except by their smaller size, since the conditions of its environment

hold in check the rapid elongation of the root, and consequently the formation of typical ringed and spiral elements. The young and absorbing roots of this species are well covered with root hairs. The cortex is loose and open, and the endodermis is a very prominent feature. The primary xylem elements vary from diarch to tetrarch. Root hairs in this section are rather scanty (fig. 14), but two may be distinguished at the top and several at the lower right of the figure.

The condition found in *S. canadensis* is similar to that already outlined for *S. tenuifolia*. There are minor differences, such as typically six protoxylem groups, which alternate with six primary phloem groups, etc. In the cortex there are six oil canals similar to those found in *S. sempervirens*. This is an exception to the general rule that roots of the Compositae which later become woody have abortive oil canals, or none at all. Root hairs are prominent in the younger plants, but have disappeared as functioning organs in the older roots, although they may cling to the surface of the root in a dried condition for a considerable time.

S. serotina, found in moist thickets and rich soils from New Brunswick to British Columbia, is permanently equipped with root hairs. The roots are very small, and come off in densely crowded rows from the short, vertical rootstock. There are typically three protoxylem groups in the young root, while in the older roots the number varies from three to five. In no instance is there marked secondary growth, which is what would be expected from the permanently hairy condition of the roots.

S. patula resembles *S. serotina* in having numerous, small, and persistently hairy roots. The ends of the roots are often glabrous, although sections made through these terminal regions show that there is no secondary growth; that is, the roots are basipilose. There are from four to six oil canals, which alternate with the protoxylem points of the woody cylinder. Still another species which resembles *S. serotina* is *S. graminifolia*. Permanent and numerous root hairs on the many slender roots are correlated with a permanently primary organization of the vascular cylinder.

In the mature roots of *S. sempervirens*, the exterior of the root is free of hairs. A transverse section through such a root, however,

makes clear the fact that in this case absence of root hairs is not correlated with extensive secondary growth. The limited amount of secondary wood in a mature root of this species is apparent in fig. 15. The five angles of primary wood, which alternate with the five bays of primary phloem just inside of five large oil canals of the cortex, may readily be distinguished. The cortex is wide, and that there are no hairs at the margin of the root is evident.

The situation occurring in a seedling root of the same species is illustrated in fig. 16. Here the four points of the protoxylem and the alternating groups of phloem are readily seen. There is a wide cortex with four large oil canals, and at the periphery a conspicuous development of root hairs. The fact that the seedling root is hirsute while the mature roots are non-hairy, and that both are without any considerable development of secondary elements, seems to point to the fact that there is a morphological correlation between the two features, and also would seem to indicate that hairs are not produced solely as the result of external physiological stimuli. This contention is further supported by the fact that when plants, collected from the Charles River Basin late in October, were brought into the laboratory and put into rich, moist humus, the new roots were as hairless as the original roots had been. Fig. 15 is a transverse section of a root of a plant collected in the Charles River Basin, where conditions were fairly dry, and not in the brackish, halophytic habitat where it may be supposed to have acquired its glabrous condition. Specimens gathered in actual salt marshes, however, showed even less development of secondary wood than is figured here (fig. 15). The seedlings with abundant root hairs, however, were collected in a salt marsh (fig. 16). Thus it would appear that a species which, through modification to environment, has in the past acquired an herbaceous type of root does not immediately develop the hirsute habit in response to change of habitat, or in response to physical and chemical stimuli only. *S. rugosa* (fig. 17) has permanent root hairs and a corresponding absence of secondary thickening. The five primary xylem points can readily be distinguished, and while there is a slight evidence of cambial activity, as might be expected at the end of the season, it will be noted that there are no true secondary elements. The outer edge

is conspicuously hairy, and the root hairs have thin walls. Both primary and secondary roots are hirsute almost to their tips.

Eupatorium

Roots of *E. purpureum*, *E. maculatum*, *E. urticaefolium*, *E. perfoliatum*, *E. sessilifolium*, and *E. altissimum* were examined. In the case of *E. purpureum*, the situation in the roots is as characteristically herbaceous as that already described for *Aster umbellatus*. Fig. 19 is a cross-section of a root of *E. purpureum* made at the end of the second season. Occupying the center of the section is the large mass of primary xylem. Eight protoxylem points can be distinguished. Even under the low degree of magnification, the slight amount of secondary growth is conspicuous. The endodermis, separating the woody cylinder from the cortex, is clearly defined, and between it and the zone of secondary elements is the phloem. Many of the cells of the cortex are filled with a dark substance, which is also found in the root hairs of the older roots, and also in the cortical cells of a related species, *E. maculatum*. This section (fig. 19) was made through the basal or proximal end of a long primary root which had no root hairs at its distal end. The persistence of root hairs for more than one season is very evident. The exodermis is a distinct feature of the topography of the root as viewed in transverse section.

Fig. 20 is a cross-section made through the proximal end of a primary root of the same species at the end of the first year. The chief difference between this and fig. 19 is that the cells of the cortex are less regular in form, and the cells and intercellular spaces have not become filled with dark substance to so marked an extent. The amount of secondary wood is limited to two or three rows of vessels. Roots of the same species at the end of the first year commonly show no development of secondary elements. Such roots are densely basipilose. Fig. 21 is a transverse section of the distal end of a root of *E. purpureum* at the end of the first year, and it is to be noted that, while there are no root hairs present at the periphery of the root, yet the vascular organization of the stele is characteristically primary. The primary xylem is indeed almost diagrammatically stellate. Fig. 22 shows this region under a higher

degree of magnification, and the complete absence of secondary elements is apparent. The persistence of the primary organization of the vascular elements and the absence of root hairs are characteristic of certain extreme herbaceous types, which may formerly have possessed root hairs at their basal end. At any rate, it is fairly clear that, if the basal region retains root hairs as permanent features of radical organization, the distal portions do not show evidence of secondary thickening, even though root hairs have disappeared; that is to say, the non-occurrence of root hairs on the outside of a root does not always indicate that the tissues inside have undergone secondary lignification.

In all the roots studied heretofore the root hairs have had thin walls. *E. purpureum* is of interest because its root hairs have very thick cell walls, although apparently the cells remain functional as long as the hairs persist. At any rate, they show no evidences of shrivelling. Some of these thick-walled root hairs are shown magnified 500 times in fig. 23. If this be compared with fig. 5, the difference in thickness between the cell walls of the root hairs of *E. purpureum* and *Aster umbellatus* will be more evident.

A species closely related to *E. purpureum* is *E. maculatum*. The leaves are thicker and more rugose, the panicle more crowded and the flowers paler. It is found in wet places, and accordingly one would not expect to find it equipped with root hairs. An examination of the roots themselves confirms this supposition. The piliferous, exodermal, and outer cortical cells are filled with a dark substance. From a comparison of the cross-section of a root of *E. maculatum* (fig. 24) with that of an old root of *E. purpureum* (fig. 20), it is evident that the central stele in both exhibits a strikingly similar topography. In both, the primary wood is so arranged that there are eight protoxylem points, and the small and relatively insignificant appearing bays of primary phloem, that alternate with the eight primary xylem angles, are indicated in fig. 24 by the darker areas just within the limits of the endodermis. Unfortunately seedlings of *E. maculatum* were not available for study and comparison. Whether they would exhibit the hirsute condition that obtained in the case of the likewise apilose *Aster puniceus* and *Solidago sempervirens*, or whether the roots are permanently with-

out hairs as are certain species of buttercup (*Ranunculus acris* for example) would be difficult to say. In view of the evidence presented by *A. puniceus* and *S. sempervirens*, it seems quite probable that the seedlings of *E. maculatum* may be hirsute.

Plants of *E. maculatum* were brought from a wet habitat into the laboratory, their old roots cut off, and the plants put into a moderately dry but rich humus. If the physiological explanation that root hairs are produced in response to a changed medium which is more favorable to their production holds, some development of root hairs might have been expected. Good roots were formed, but neither as a result of wounding, nor in response to a change of environment, were root hairs formed. Thus it would seem that the non-hairy habit is one of long standing, and that the morphological correlation of root hairs and primary wood is well established. Once a plant has developed hairs, which remain functional for a considerable period, it seems to indicate that there is a correlated inhibition of secondary growth. Primary organization of the radical stele having become a habit as it were, the plant continues to omit the production of secondary growth even when it no longer develops root hairs.

The common buttercup presents an illustration of a plant that has lost root hairs even in the young condition, while yet retaining only primary organization in its radical stele. It seems likely, in view of the evidence supplied by the Compositae, that its ancestors may have possessed root hairs and yet have lost them, while retaining a primary steler organization after some such fashion as has been described in the case of *Aster puniceus* and *Solidago sempervirens*. Extreme herbs of the monocotyledonous type which never have secondary wood, of course are often characterized by the presence of conspicuous root hairs. This fact is well attested by the diagrams in most of the standard textbooks of botany, but the definite correlation of root hairs with the absence of secondary growth, so far as I have been able to ascertain, has not been emphasized. This condition apparently was first noted by JEFFREY and TORREY (3).

Fig. 25 represents a cross-section of a mature root of *E. urticaefolium*. In the center there is a six-angled mass of primary xylem,

and alternating with its protoxylem apices are six semilunar masses of primary phloem. There are no secondary elements, and the root hairs are long and as conspicuously thin-walled as were those shown in fig. 5 for *Aster umbellatus*.

The common boneset or thoroughwort, found in meadows and low grounds, illustrates a situation common in the asters. The young roots are consistently hairy, although the plants grow in swampy places, and the hairs are thin-walled. The characteristic shape of the primary xylem mass in young roots is triangular, and resin canals are conspicuously absent. Where there is only a small amount of secondary growth the root hairs persist, but in older roots which get to be very woody, the root hairs disappear entirely.

An example of an almost completely woody type of root is found in *Eupatorium sessilifolium*, a very tall plant with sessile, sharp, pointed, opposite leaves. It is found in copses and dry banks where root hair production might be expected. The amount of secondary thickening, however, is greater than in any other species studied, the primary elements being confined to the very small center of the woody cylinder. The cortex is correspondingly reduced in thickness. As even the youngest roots were without root hairs when the specimens were collected, it would seem that cambial activity is initiated at an early stage in this species. Another interesting feature is the trace in the larger and more woody roots of the beginning of a layer of periderm. As is well known, roots of trees and certain plants that grow for many years are protected outwardly by a corky jacket after they have ceased to function as absorbing organs. Still another feature is the presence of large rays such as are characteristic of woody forms, usually of the aggregate type. Similar rays are to be noted in *E. perfoliatum*. Another species with woody roots is *E. altissimum*. In the young roots there is a clearly defined primary xylem region with six points. Root hairs are numerous. Later, when the secondary elements are formed, the root hairs become non-functional, although they are not easily sloughed off. As the cylinder becomes more woody they shrivel up, but in most cases they do not drop off. Rays are prominent, and the cortical cells are thickened so as to give them

a diamond-shaped appearance. The result is an openness of cortical structure that resembles that found in plants growing in moist places.

Vernonia

Three species of Vernonia, collected from the Botanical Gardens, were studied. They were there listed as *V. crinita* var. *Baldwini*, *V. altissima*, and *V. arkansana*. Whether *V. crinita* var. *Baldwini* is the recognized *V. Baldwini* Torr., or whether the *V. arkansana* listed by the Garden as such is the same as *V. crinita* Raf., would at this time be hard to determine.[1] All three species have unusually large roots, which are permanently and densely hairy, and as this is the feature that is of interest in the present connection, I shall follow the nomenclature adopted by the Botanical Garden of Harvard University.

V. crinita var. *Baldwini* has very large roots which are persistently hirsute, especially at the basal or proximal end. Even at the close of the season's growth there is little or no secondary wood, and as a result the five points of the primary xylem stand out conspicuously in cross-section. Fig. 27 represents a transverse section of a root of this species, and here is shown what may be called the maximum of secondary development. The cortex is wide, as in roots of the herbaceous type, many of the cells being filled with a dark secretion apparently similar to the secretions in the cortical cells of *Eupatorium purpureum* and *E. maculatum*. The cortex is further characterized by the presence of scattered stone cells. The exodermal layer is sharply defined, and in many instances is filled with the same dark substance that is to be noted in the cortical cells. The piliferous layer is composed of thin-walled cells. The situation is similar in the younger roots and the distal portions of older roots. Fig. 28 is a transverse section through the distal region of a basipilose root of the same species (*V. crinita* var. *Baldwini*)

[1] At the time this paper was written (March-April 1921) the *Vernonia* plants had not appeared above the ground, and hence it was not possible to determine what they were at that time. In mid-June, however, the identity of the first two species was determined by Professor FERNALD, who ascribed *V. crinita* var. *Baldwini* to the species *V. interior* Small, and *V. altissima* to *V. illinoensis* Gleason. Owing to the absence of the tops of *V. arkansana* at that time, it was necessary to accept the nomenclature of the Harvard Botanic Garden for the third species.

gathered late in autumn. Here the arrangement of the primary elements is strikingly diagrammatic. A few root hairs may be noted at different points on the periphery. Nearer the base of the root these are more numerous, while farther away from the point of attachment the root is almost entirely lacking in hairs. *V. altissima* (fig. 26) has even larger roots than *V. crinita* var. *Baldwini*. There is practically no secondary wood, and the roots are very hairy. The wide cortex with darkly filled cells is a conspicuous feature of the cylinder. *V. arkansana* is similar in organization to both these species. It has the largest root in diameter of the three. In cortical structure it is more like *V. altissima*, in steler topography more like *V. crinita* var. *Baldwini*.

Helianthus

Only one species was examined, *Helianthus orgyalis*. Fig. 18 represents a transverse section of a root, in the center of which the six-angled primary xylem mass may readily be distinguished. There are no oil canals in the cortex alternating with the apices of the xylem groups, but the phloem can easily be determined. There is only a slight amount of secondary wood. The root hairs are numerous, long, and thin-walled. The hairs clung so closely to the soil particles that not even washing, fixing, and imbedding served to remove all the dirt, some of which may be noted still adhering.

Chrysanthemum

Two species of *Chrysanthemum* were studied. One was a garden variety, probably a hybrid, the other was *C. uliginosum*. The former had hairless roots which proved to be very woody; the latter, which had hairs, was almost entirely without secondary thickening. The roots were hairy from base to tip. The protoxylem elements were arranged in four groups. The distal parts of some roots were swollen into little tubercules, evidently caused by the intrusion of a unicellular organism of some kind, with the result that the cortical region, and the tracheal elements also, had undergone considerable disintegration of structure. This aspect of the case, as it seemed to have no bearing on the production or suppression of root hairs, is merely noted in passing.

Dahlia

Two species of *Dahlia*, growing in the garden, were examined, and the distribution of root hairs was found to be the same as in the other genera already described. Thus *Dahlia*, while contributing nothing new to the results recorded here, confirms them in an interesting way. There was comparatively little secondary wood, and root hairs were persistent, noticeably at the base of the primary and secondary roots. One feature of interest was the presence of primitive oil canals in the endodermis, a situation obtaining also in *Cynara* and species transitional between the Tubuliflorae and the Liguliflorae.

Lysimachia

Although the present investigation was made chiefly on the Compositae, numerous and permanent root hairs were noted on certain species of *Lysimachia*, both on the roots and rootstocks. It would be of interest to see whether other species of the family might not exhibit the same phenomenon.

Leguminosae

McDOUGALL (5) reports finding persistent root hairs on *Gleditsia triacanthos*, and less perfect, but still permanent ones, on *Cercis canadensis* and *Gymnocladus dioica*. He noted that the root hairs not only extended back a considerable distance from the tips of the roots, but that they were present on nearly "all the smaller parts of the root system," and that they persisted "as long as the root epidermis, whether this be for a few weeks or for several months." Whenever root hairs were a constant feature, as in *Gleditsia*, they were observed to be characteristic of the roots of trees, "in various localities and in very diverse habitats, the habitats ranging from the climax upland forest of Champaign County, Illinois, to the typical bottomland forests along the Vermillion River in Vermillion County, Illinois," and to occur at as great a depth as four feet, as well as near the surface. McDOUGALL states that the root hairs are thick-walled, the average width being 2 μ, which he says is four times the thickness of the young cell walls in the same species. His conclusion is that "the thick-walled root

hairs are considered xerophytic structures, and are believed to be relics of a time when the species which possess them grew only under xerophytic conditions."

Since McDOUGALL's paper appeared I have examined roots of the three leguminous species in which he reported finding permanent root hairs, and have found that all three species, but especially *Gleditsia triacanthos*, have persistent root hairs on the smaller roots.

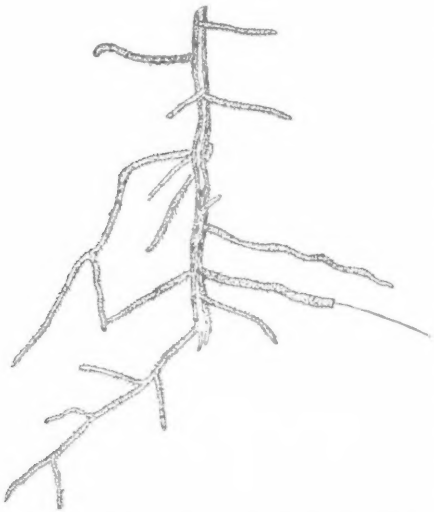


FIG. 1.—Portion of root of *Gleditsia triacanthos*, showing permanent root hairs.

In view of the previously mentioned results in certain species of Compositae, the situation in the woody cylinder was examined with interest. It was found that the hairy roots of *G. triacanthos* had a very slender woody cylinder. Text fig. 1 shows a portion of the terminal region of the root system of a very large honey locust. At the right one of the roots has been divested of its cortical jacket, and the woody cylinder appears as a very slender thread as a result. Transverse sections were made through the younger and more distal parts of the roots which were hirsute, and also through the larger and older roots which did not exhibit hairs exteriorly. The former showed a typical herbaceous organization, that is, where root hairs were present there was little or no secondary thickening. In older roots, however, where secondary growth was well developed, root hairs had disappeared, and there was a jacket of periderm or cork around the outside, similar to that found in mature roots of most arborescent species. Thus McDOUGALL's work confirms in an unexpected and interesting way the results of the present investigation.

Fig. 29 represents the central cylinder of one of the small hairy roots of *Gleditsia triacanthos* under a high degree of magnification (about ×250), and it is quite clear that the woody cylinder is composed of only primary wood. The organization is diarch, that is, there are two protoxylem clusters. Fig. 30 represents a few of the cells at the periphery of a root of the same species, and several of the root hairs under a high degree of magnification (×500). It would not appear from this section that the cell walls are conspicuously thickened. At any rate, they are no thicker than the neighboring cortical cells, and compared with the root hairs of *Eupatorium purpureum* under the same degree of magnification (fig. 23) they seem relatively thin-walled. In fact, when this figure is compared with fig. 5, which represents some of the root hairs of *Aster umbellatus*, it does not appear that those of the locust are conspicuously thicker than those of the aster. The degree of magnification is the same in both instances.

In this connection it may be emphasized that even in large trees these general principles for herbaceous roots hold true, namely, that persistent root hairs and absence of secondary growth in roots are significant and correlated phenomena.

Discussion

It is a generally accepted fact that the presence of root hairs in some way is correlated with the process of absorption. Whether root hairs are produced and suppressed in response to changed physical and chemical conditions, and whether more root hairs are produced in a dry soil or in a moist soil, or a soil rich in food salts, need not be discussed here, since physiological data do not seem to be in agreement on these points. The outstanding physiological explanations of the presence of root hairs have been summarized already. That, however, there is a definite correlation between the absence of secondary growth (illustrated particularly in certain species of the Compositae) and the presence of persistent root hairs seems evident from the preceding descriptive data.

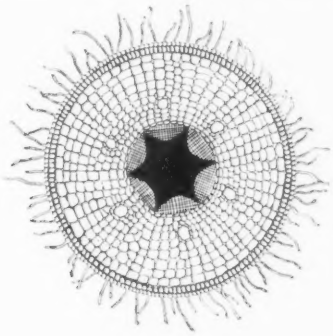
The occurrence of only primary wood in the young roots of plants (with the notable exception of the conifers) which are provided with a region of root hairs just behind the growing point is commonly recognized. This situation, where only primary

wood and primary phloem are present, is shown diagrammatically in text fig. 3. In the center is the primary xylem (represented in solid black), and alternating with its projecting points are the six bays of primary phloem (cross lined). Just outside the vascular cylinder is the endodermis, a constant structure in roots, which separates the conducting tissues from the storage elements of the cortex. There are also six oil canals, which are a characteristic but not a constant feature of the root organization of the Tubuliflorae. The cortex is wide in extent and ends peripherally in a series of horizontally elongated cells, the root hairs. Where the hirsute condition is of short duration, and just behind the growing point of the root, it may be designated as punctipilose.

FIG. 2.—Diagrammatic representation of distribution of root hairs in *Solidago rugosa*, from plant collected late in autumn of 1920; root hairs persist nearly to tips of roots, and are present on slender secondary roots; note that tips of floral branches extend out nearly to limit of absorbing region.

In certain herbaceous roots, notably the Compositae, however, the root hairs persist for weeks or even longer. Sometimes, as in *Solidago rugosa*, the roots are hirsute almost to their tips, this situation obtaining in roots that are fairly short and slender. *S. serotina* and *S. patula* are good examples of plants with numerous, short, slender roots that are densely pilose to the tip. The distribution of such a root system is shown in text fig. 2, which represents a simplified condition of the root system of *S. rugosa*. It can be seen that

the roots are slender and not very long, and that they are consistently hairy from the point of attachment to the main axis to the distal part of the root. It is to be noted that the angle of attach-



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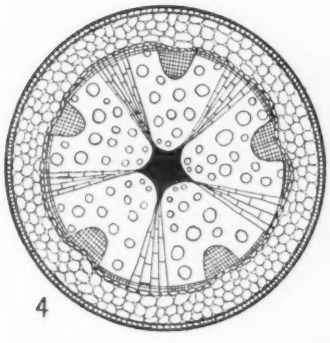

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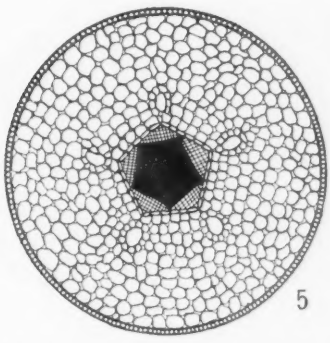

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FIGS. 3–5.—Fig. 3, transverse diagram of permanently hirsute root, showing absence of development of secondary elements, this situation obtaining in young roots also; primary xylem shown in solid black. Fig. 4, old and woody root of herbaceous *Aster*, diagrammatically shown; primary xylem depicted in black in center and alternating bays of primary phloem shown imbedded in secondary elements near cortex. Fig. 5, permanently herbaceous root, without hairs and without secondary thickening, which may have been derived from herbaceous hirsute type by loss of absorbing peripheral cells.

ment and the vertical orientation of the leaves are such as to direct the flow of water collected during a rainy period down the axis of the stem, from whence it would naturally be distributed from the

axis outward. The development of root hairs seems to be coordinated in some species with this method of shedding water.

Where the root system is extensive and extends far beyond the shadow of the leafy crown at noon, the distribution of hairs is quite different. Text fig. 6, which is a conventionalized diagram of *Eupatorium*, shows that root hairs are present only near the base of the stem. It will be noted that the leaves are numerous, large, and verticillate, particularly in the case of *E. purpureum*. It is reasonable to expect, then, from the nature and disposition of the leaves, that during rainy periods the water which runs down the main stem would supply those portions of the root which are nearest to the aerial axis. Accordingly, this region where there is likely to be the greatest amount of available moisture is provided with root hairs. Roots which are hairy at the proximal end and glabrous distally may conveniently be designated as basipilose. Many species in which the roots are not hirsute in the adult condition show a basipilose arrangement of root hairs in the seedlings, as for example, *Aster puniceus* and *Solidago sempervirens*. Thus the generalization that root hairs appear only behind the growing point (punctipilose) and persist only for a brief time obviously does not always accord with the facts as exhibited in a highly herbaceous family like the Compositae.

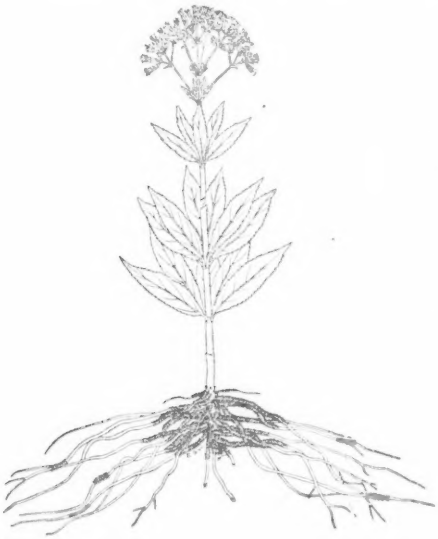

FIG. 6.—Diagram of root system of *Eupatorium purpureum*, illustrating basipilose condition of roots, and smooth distal appearance of such roots with exception of scattered patches of hairs.

The persistence of basipilose root conditions in the seedlings of plants which, in a mature state have bald roots but at the same time a non-woody vascular organization, is of interest. It may be assumed, on the basis of the doctrine of recapitulation (**2**), that in extremely herbaceous roots (as for example the roots of certain species of *Ranunculus* which are never hairy) the non-hirsute condition has been reached by way of the basipilose type of herbaceous root. This assumption of the origin of hairless herbaceous roots from a primitively basipilose condition is further strengthened by a study of the internal structure of the roots. Text fig. 3 represents diagrammatically the situation in a year old root of *Helianthus orgyalis*. Here the permanently basipilose condition is accompanied by the absence of secondary elements. The advantage of such a situation in connection with water absorption and transfer is obvious (**3, 12**). Text fig. 5 represents the condition of an herbaceous root without root hairs which has probably originated from the persistently basipilose type. The primary xylem is indicated by solid black, and the alternating five groups of phloem are cross hatched. This is the vascular organization characteristic of *Ranunculus acris* and *R. repens* roots.

The woody root, characteristic of most trees, of certain asters, goldenrods, etc. (for example, *Aster Shortii*, *Solidago tenuifolia*), is shown in diagram in text fig. 4. The primary xylem is shown in the center (black). It is five-angled, and alternating with its projecting points are the secondary vascular bundles, indicated by the presence of vessels. Between the vascular groups originated by cambial activity are to be seen five large rays. Imbedded in the secondary wood, just inside the endodermis, are the five groups of primary phloem (cross hatched). The cortex is considerably reduced in extent and importance, storage being cared for in the secondary cylinder. In very woody species a jacket of periderm is developed at the periphery of the root, which effectively checks absorption. The function of roots of this kind is clearly mechanical and conductive. Woody roots, in the young condition, were distally hirsute (punctipilose), and the root hairs were relatively ephemeral structures.

The herbaceous type in stems is characterized by a marked decrease in woody tissue, and by a corresponding increase in parenchymatous elements connected with and related to the outgoing leaf traces. The leaf traces become larger and more numerous, until they are equal in size and number to the stem bundles. The foliar traces, however, frequently differ from the normal cauline segments by the absence of a cambium. Obviously it would be a distinct disadvantage for the parts of the cylinder connected with the conduction of food to be capable of radial increase. Thus extreme herbaceousness in stems is marked by two features: (1) increase in size and number of the foliar traces with a corresponding loss of cambial activity, and (2) the transformation of more and more woody tissue connected with the outgoing leaf traces into storage tissues, until, in extreme herbs and very thin stems, the parenchymatous elements flank but do not subtend the leaf traces.

In a similar way extreme herbaceousness in roots is also marked by the absence of secondary growth. Lessened cambial activity in the root is correlated with the tendency to persistence of the root hairs, the advantage from the point of view of the ready transfer of water in the case of roots with only primary outgrowth being obvious.

Summary

1. The fact that root hairs are not always ephemeral structures is well exemplified in certain species of Compositae in which they persist for one, two, and sometimes even for three years.

2. Persistent root hairs are also found in the Leguminosae, notably in *Gleditsia*, and are probably of wide occurrence.

3. In roots which are permanently hairy the hirsute region may be general, or it may be limited to the basal or proximal region of the root system.

4. Roots of the second category are apparently found only in extreme herbs. Such roots may be conveniently designated as *basipilose*.

5. The basipilose condition is apparently correlated with the mode of shedding water from the main axis.

6. Internally the extreme type of herbaceous root is characterized by a conspicuous absence of secondary thickening.

7. Secondary thickening marks the disappearance of the root hairs, and usually the root becomes jacketed with periderm. Such roots are incapable of absorbing water except at the tips of the roots, which are provided with root hairs. Such roots may be designated as *punctipilose*.

8. Some roots which are permanently without secondary thickening are likewise without root hairs. Such roots may be described as *apilose*, and probably the ancestors of such roots were basipilose.

9. The herbaceous type, both in root and stem, is characterized by decreased cambial activity and a reduction in amount of secondary growth.

10. In the stem herbaceousness is associated with the multiplication of leaf traces and the transformation of woody into storage tissues.

11. In the root the herbaceous type is characterized by the correlation of the presence of permanent root hairs, and a marked decrease in or absence of secondary growth.

I wish to thank Dr. E. C. JEFFREY for valuable advice and assistance rendered during the course of this investigation. I also wish to thank Mr. JAMES AUSTIN for help with the technical preparations and for aid in making the photomicrographs.

HARVARD UNIVERSITY

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EXPLANATION OF PLATES I–V

FIG. 1.—Transverse section of root of *Aster umbellatus* at end of second year; ×60.

FIG. 2.—Transverse section of root of same species at end of first year; ×60.

FIG. 3.—Transverse section of root of same species growing in swamp; ×60.

FIG. 4.—High power magnification of woody cylinder of year-old root of *A. umbellatus*, showing absence of secondary growth; ×250.

FIG. 5.—Detail of edge of root of same species at end of first year, showing persistent root hairs; ×500.

FIG. 6.—Transverse section of year-old root of *A. tataricus*, showing only primary wood in center; ×40.

FIG. 7.—Transverse section of root of *A. Shortii*, illustrating absence of root hairs where there is conspicuous development of secondary wood; ×40.

FIG. 8.—Younger root of same, showing abundant root hairs and slight development of secondary elements; ×60.

FIG. 9.—Transverse section of mature root of *A. novae-angliae* with well developed secondary wood; ×40.

FIG. 10.—Transverse section of young root of New England *Aster* with numerous root hairs and small amount of secondary thickening; ×60.

FIG. 11.—Transverse section of mature root of *A. puniceus* with no root hairs and small amount of secondary growth; ×40.

FIG. 12.—Root of *A. puniceus* seedling, showing root hairs and slight amount of secondary growth; ×40.

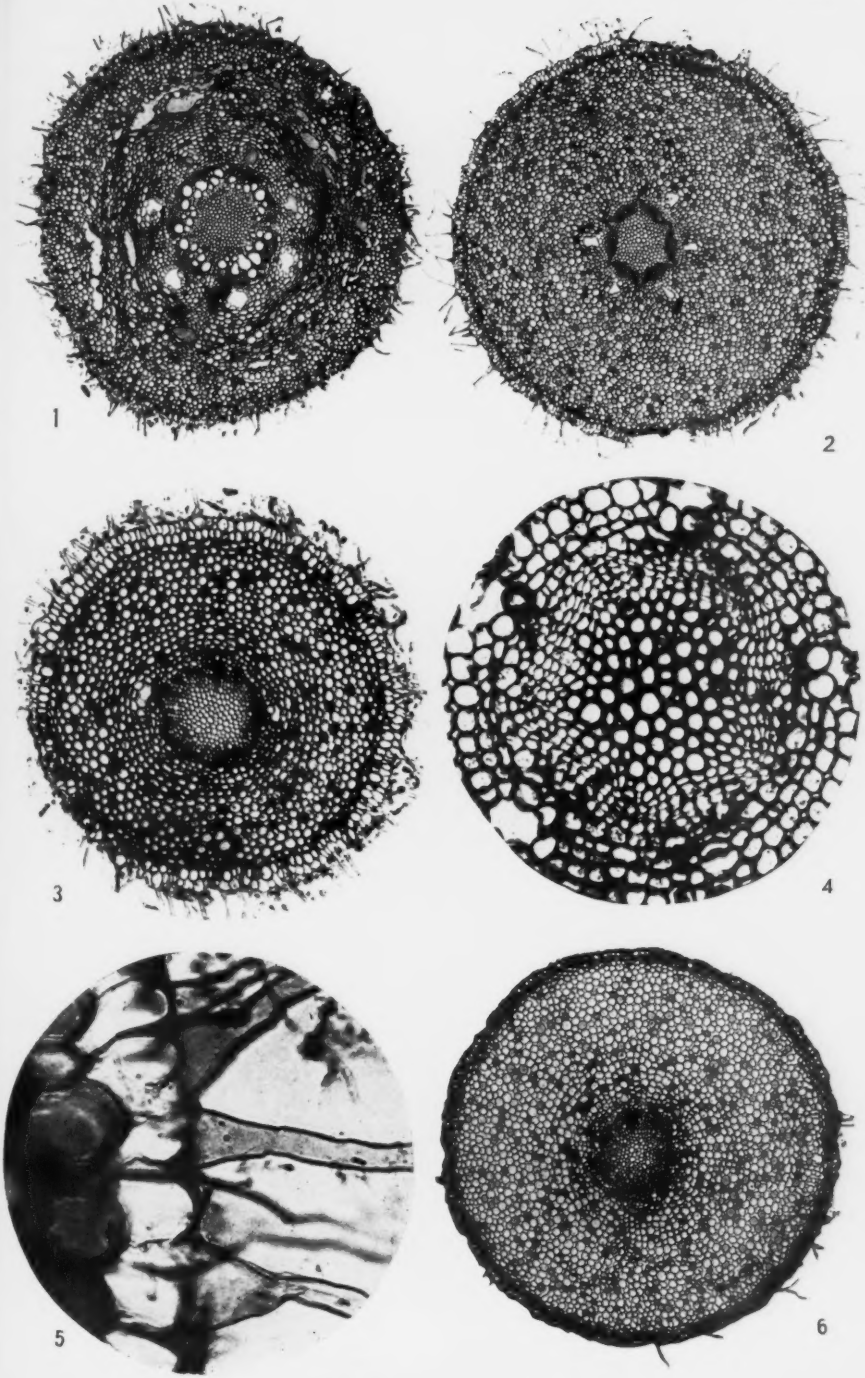
FIG. 13.—Transverse section of mature root of *Solidago tenuifolia* with well marked development of secondary wood; ×40.

FIG. 14.—Young and absorbing root of same, with small primary xylem cylinder and root hairs; ×80.

FIG. 15.—Mature root of *S. sempervirens* with small amount of secondary growth and no hairs; ×40.

FIG. 16.—Root of seedling of *S. sempervirens*, showing well developed root hairs and conspicuous absence of secondary elements; ×60.

FIG. 17.—Transverse section of root of *S. rugosa*, with root hairs and without secondary growth; ×60.



WHITAKER on ROOT HAIRS

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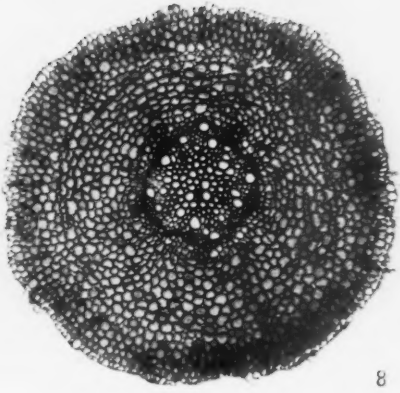

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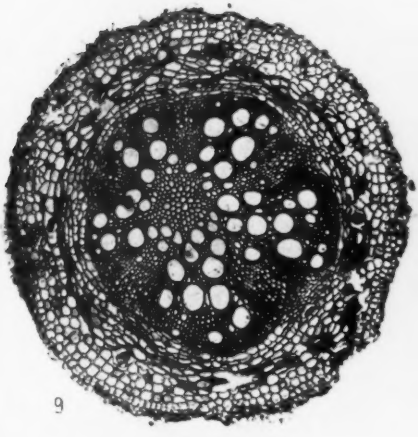

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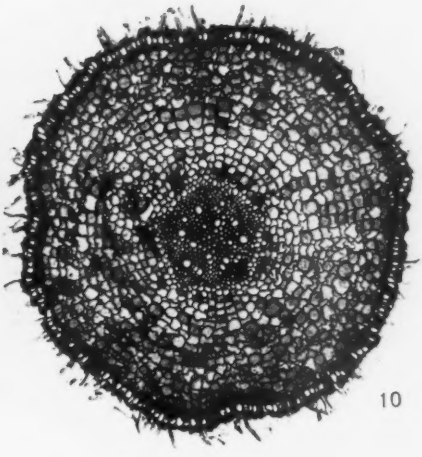

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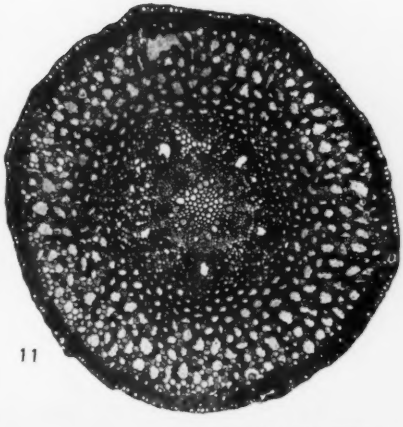

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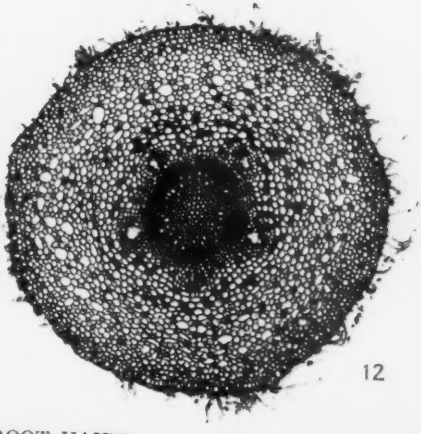

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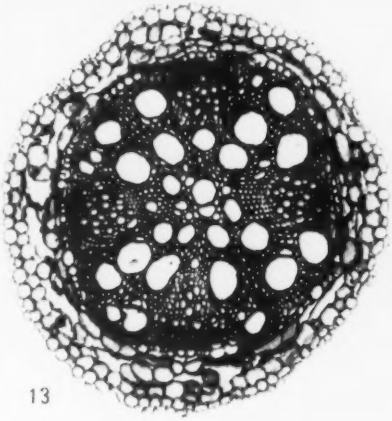

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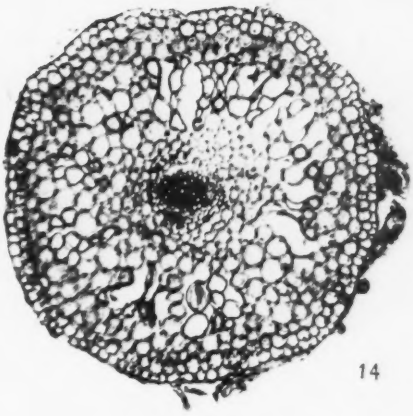

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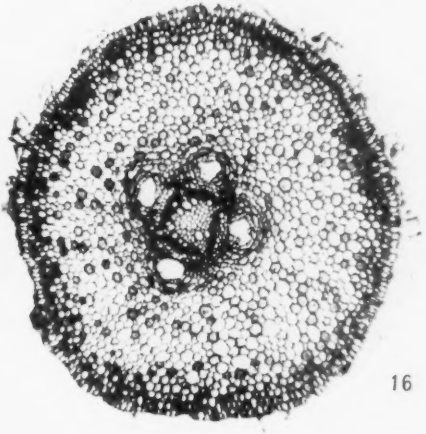

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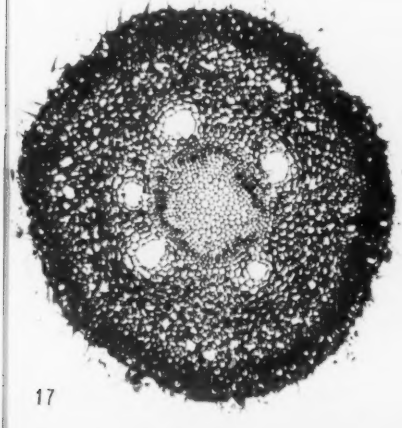

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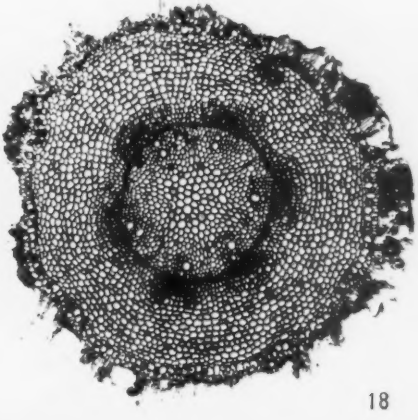

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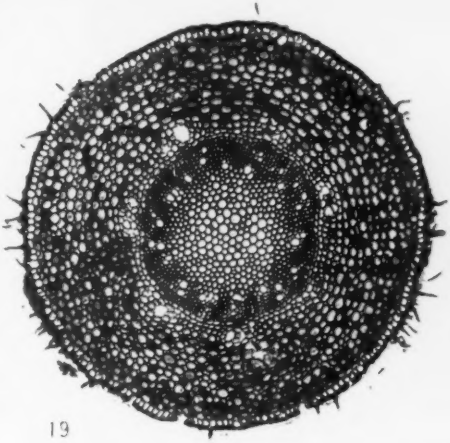

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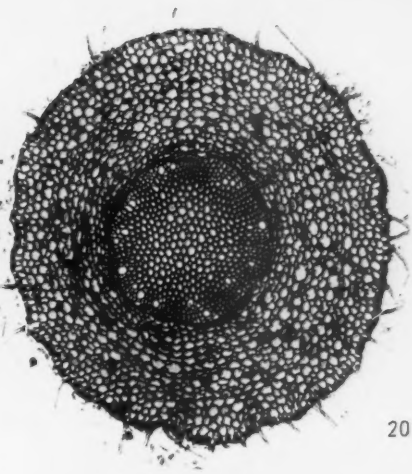

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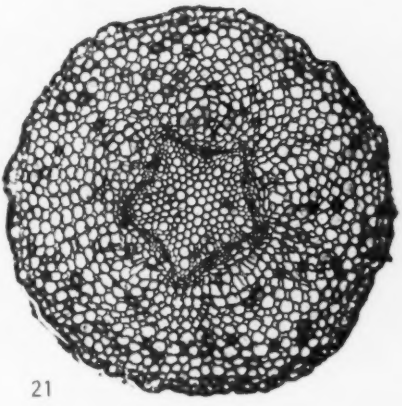

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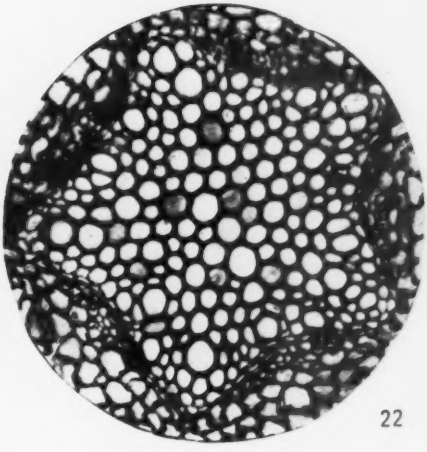

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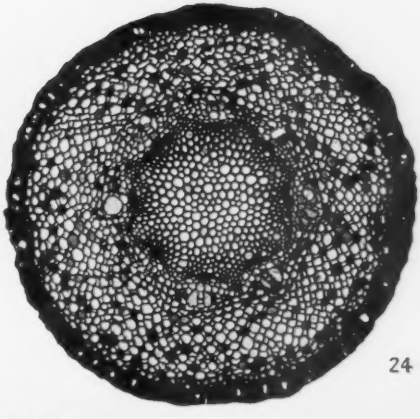

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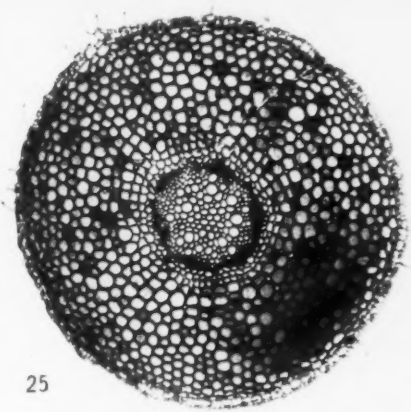

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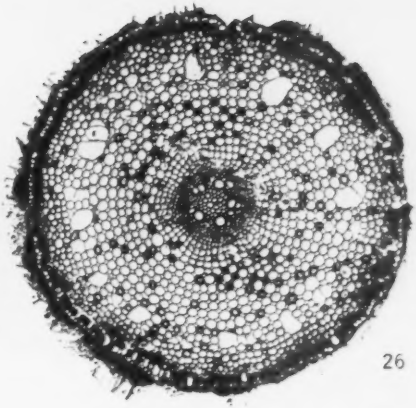

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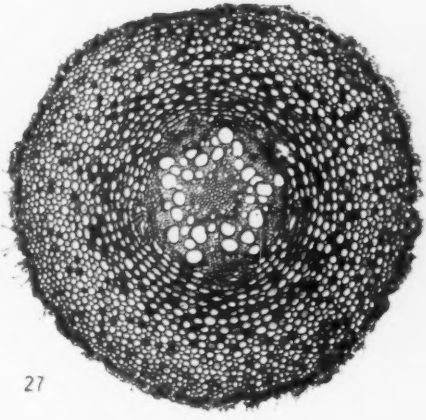

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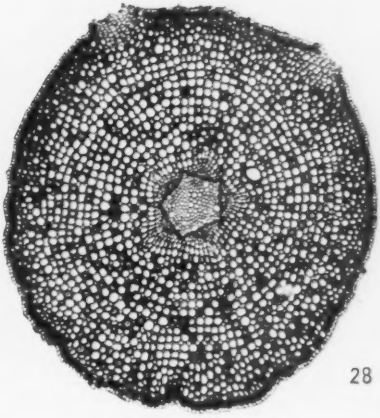

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WHITAKER on ROOT HAIRS

FIG. 18.—Transverse section of mature root of *Helianthus orgyalis*, in which six segments of secondary wood stand out in contrast with angles of protoxylem elements; abundant root hairs; ×40.

FIG. 19.—Transverse section of root of *E. purpureum*, made at end of second year; ×40.

FIG. 20.—Transverse section from root of same species at end of first season; slight development of secondary wood and presence of root hairs characterize specimen; ×40.

FIG. 21.—Transverse section of terminal region of root of *E. purpureum* at end of first year; no root hairs or secondary growth; ×40.

FIG. 22.—Woody cylinder of same species under higher degree of magnification; ×250.

FIG. 23.—Portion of piliferous layer of year-old root of *E. purpureum*, highly magnified to show thick-walled character of root hair; ×500.

FIG. 24.—Transverse section of mature root of *E. maculatum*, showing absence of both root hairs and secondary growth; ×40.

FIG. 25.—Mature root of *E. ageratoides* in transverse aspect, showing persistent root hairs and slight secondary increase; ×60.

FIG. 26.—Transverse section of very large mature root of *V. altissima;* ×20.

FIG. 27.—Transverse section of basal region of root of *V. crinita* at end of first season; ×20.

FIG. 28.—Young root of same species, showing condition obtaining in young roots and distal end of roots at end of first season; ×25.

FIG. 29.—Transverse section of woody cylinder of root of *Gleditsia triacanthos*, showing primary organization of tissues; ×250.

FIG. 30.—Peripheral edge of root of same species, showing persistent root hairs; ×200.

MATURATION AND GERMINATION OF SEEDS OF ILEX OPACA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 308

SUMNER ALBERT IVES

(WITH FIVE FIGURES)

Introduction

In central North Carolina the blossoms of *Ilex opaca* Ait. appear late in April. By the middle of June there are well formed berries, which turn red in December, and are shed the following spring. Since all the ordinary methods of immediate germination fail, this species has never been grown from artificially germinated seeds, and nurserymen are unable to produce their stock from seed, depending entirely upon seedlings and young trees gathered in the forest to supply the trade. The holly seed, therefore, presents another case of delayed germination, and these investigations have sought to discover the causes of the delay and the methods by which it may be overcome. There is no literature dealing with the germination of seeds of *Ilex*, but the literature dealing with the delayed germination of other types will be briefly summarized.

The first important contribution to our knowledge of the causes of delayed germination was made by CROCKER (2), who showed that in many instances the delay in germination is due to the structure of the seed coats, which exclude water or oxygen to such an extent that germination is suppressed. Some years later, in working with the seeds of *Alisma Plantago*, CROCKER and DAVIS (4) determined that the delay in germination is due largely to the mechanical resistance of the seed coats, and that the action of acids and bases in increasing germination consisted of a weakening of the colloids of the seed coats rather than stimulation of the embryo. That the delay in the germination of the dimorphic seeds of *Xanthium* is not necessarily entirely a coat effect was shown by SHULL (12), who found that the upper and lower seeds have differ-

ent oxygen requirements, and that the embryo differences act with coat differences to effect the delay.

No recent literature which gives the structural and microchemical changes taking place in the developing of the immature embryo can be cited, but another factor in delayed germination, after-ripening, has received considerable attention. *Crataegus* has a seed similar in appearance to the holly, with berry-like fruit inclosing bony covered seeds. The fruit of the hawthorn is a pome and ripens in September, whereas the fruit of the holly is a berry-like drupe which ripens in winter and early spring. DAVIS and ROSE (**5**) showed that although the embryo is mature it will not germinate unless subjected to a season of cold. An exposure in the imbibed condition to 5°–6° C. for 75–90 days proved to be the best for after-ripening. Alternate freezing and thawing was instrumental in rupturing the seed coverings, but was not as good for after-ripening as the constant cold temperature. The chemical changes in the after-ripening period of several species of *Crataegus* were followed microchemically by Miss ECKERSON (**6**), who found that the stored food in the embryo was a fatty oil with no starch or sugar present. In general this agrees with the situation in *Ilex*, except that in *Ilex* the food is stored in the endosperm instead of the embryo. The initial change in the after-ripening of *Crataegus* seeds is an increase in water-holding capacity and a greater catalase and peroxidase activity. Toward the end of the after-ripening period oxidase is manifest, and as the fats decrease sugar appears. The after-ripening can be shortened greatly by soaking the seeds for 12–24 hours in dilute acids. The seeds of *Avena fatua* require a season of after-ripening which was shown by ATWOOD (**1**) to be independent of the water content or the light exposure. By breaking or searing the seed coats and increasing the supply of oxygen, the delay in germination can be greatly restricted. Although *Juniperus* is widely removed taxonomically from *Ilex*, yet in the main the seeds of each possess the same features. In the former, however, the embryo is mature, while in the latter it is very immature. The changes enumerated by PACK (**11**) as accompanying after-ripening, especially the decrease in stored fats and increase in sugar together with an increase in amino acids, follow

closely those observed in the endosperm of the *Ilex* during the development of the embryo. He finds that a continuous cold of 5° C. is the best temperature for germination.

A summary of the means by which seed dormancy is secured by plants is given by CROCKER (3). He mentions five primary causes of dormancy: rudimentary embryos, complete inhibition of water absorption, mechanical resistance of inclosing structures, encasing structures interfering with oxygen absorption, and a state of dormancy in the embryo itself. He states further that a combination of two or more of these primary causes and an assumption of secondary dormancy might be included in the list. *Ilex* illustrates the combination of two primary causes of delay, immaturity of the embryo and mechanical resistance of the structure inclosing the embryo. The forcing agents which CROCKER suggests, such as acids, bases, salts, freezing and thawing, constant low temperatures, alternation of temperatures, light, and oxygen, all have been tried on holly seeds. In addition electrical stimulation, organic compounds such as sugar and organic acids, etherization, and enzymes have been used in attempts to force these seeds to germinate.

Materials and methods

The seeds of *Ilex* used in this work were collected from various localities, as indicated in table I.

TABLE I

COLLECTIONS OF HOLLY MATERIAL

No.	Condition	Locality	Date	Storage
1	Ripe berries	N. Carolina	April, 1918	Cleaned, air dried
2	Ripe berries	N. Carolina	Feb., 1920	CS_2 treated, dried
3	Cleaned seeds	N. Carolina	April, 1920	Imbibed in icebox
4	Berries (from 5 counties)	Alabama	Jan., Feb., 1921	Air dried
5	Ripe berries	N. Carolina	April, 1921	Icebox
6	Green berries	N. Carolina	June, 1921	Icebox
7	Berries (from 11 counties)	Alabama	1921–1922	Air dried
8	Ripe berries	N. Carolina	June, 1922	Air dried
9	Soil (from under holly trees)	Ala., Fla., N.C.	May, 1921	Sealed jars

The seeds were freed from pulp either by macerating the berries in water and scrubbing them clean under the faucet, or by stirring

the berries rapidly for two hours with coarse sand and water. After cleaning they were dried in small quantities, winnowed, and stored for use as indicated in table I. The seeds were set to germinate in Petri dishes on sterile cotton or filter paper. Each culture consisted of 50 whole berries, 50–100 cleaned seeds, or 10–25 seeds without pericarps. The removal of the pericarps was facilitated by a period of drying, after which they could be cut off without injuring the embryo. The facilities for low temperature experiments, from −5° C. to +10° C., were provided by the Bionomics Greenhouse, and those from 20° to 40° C. by the Hull Botanical Laboratories.

For constant illumination, a box was devised which kept the seeds in light of about 25 foot candles. Simple methods of stimulating the seeds electrically and abrading them mechanically need no description. Increased supplies of oxygen were obtained by setting the seeds to germinate in vessels containing Oakland dioxogen, or by immersing the seeds in 25 per cent dioxogen. Examination of the seeds was made at seven day or thirty day intervals, according to the rate of development. Each examination consisted in making a microscopic and microchemical study of freehand sections, 20–40 μ thick, cut longitudinally through the embryos of a number of seeds. The microchemical methods of Miss ECKERSON (7) have been followed for the presence, distribution, and changes in storage substances and minerals.

Temporary mounts were made by placing the sections on the slide in a drop of an alcoholic-glycerin-glacial acetic acid-formalin solution which kills, fixes, clears, and preserves. Permanent mounts were prepared whenever an appreciable advance in development was observed. The procedure followed was to wash the sections with alcohol for ten minutes, stain them one minute in alcoholic eosin, rinse five minutes in alcohol, and then dehydrate, clear, and mount in balsam. Camera lucida drawings of uniform magnification were made of each stage examined.

Results

MORPHOLOGY.—The mature seeds of *Ilex* are bright red. The shape is globose, with a polar diameter of about 10 mm. and an

equatorial diameter of 9 mm. Inclosed in a sweetish pulp are four ribbed nutlets, within which are the seeds proper. The entire fruit is a berry-like drupe. At the time the berries fall from the

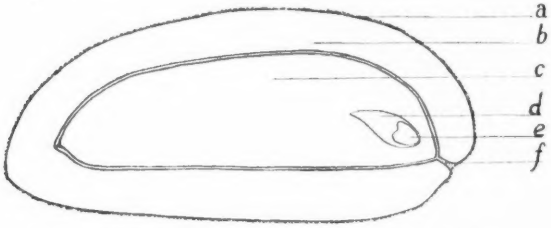

FIG. 1.—Longitudinal section of entire seed at time of shedding: *a*, remains of pulp; *b*, woody pericarp; *c*, endosperm; *d*, cavity around embryo (*e*); *f*, pectic micropylar plug.

tree the size of the endosperm is about 5 mm. × 1 mm., and the volume of the embryo is not more than 0.00004 that of the endosperm. The embryo is somewhat heart-shaped, with no hypocotyl or plumule, and only the beginnings of cotyledons (fig. 1).

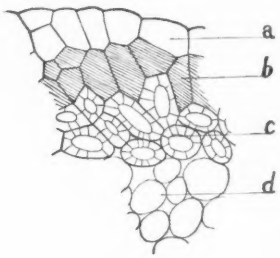

FIG. 2.—Section through outer part of fruit: *a*, cutinized epidermis; *b*, hypodermal anthocyanin; *c*, sclerenchymous cells; *d*, thin-walled sugary parenchyma.

The outermost layer of cells forms a cutinized epidermis, and the red color is due to hypodermal anthocyanin. Between the colored cells and the pulp is a double row of sclerenchymous cells. The pulp itself consists of thin-walled, loosely-joined cells rich in dextrose, with some fructose (fig. 2).

The hard material of the ribbed nutlets is mineralized lignin. Outside of this is an irregular pectic layer, and inside another pectic layer, and then one of lignin. These four layers comprise the pericarp. The seed proper, composed of endosperm and minute embryo, is surrounded by two layers respectively, one of pectic and the other of suberized substances. The cell walls of the endosperm are cellulose. The cells are largely filled with aleurone grains or protein-oil bodies. No starch is present, but minute

quantities of sugar appear in the coats and in the outer cells of the endosperm (fig. 3).

MICROCHEMICAL STUDIES.—In 1918 a series of tests was run with the seeds of collection no. 1, and microchemical determinations made each week for changes in fats, sugars, and proteins. It was found that at all temperatures the fat becomes more and more fluid around the embryo, and finally disappears in the region between the hypocotyl and the micropyle in from thirty to sixty days. In general the higher the temperature the more rapidly the fat is hydrolyzed. There is no sugar present in the endosperms of fresh seeds, but as the fat disappears sugar is formed. Apparently also some sugar comes in from the pectic coats, which are rich in dextrose and dextrin. With the Biuret test the protein of the endosperm shows progressively more and more amino acids in the region around the embryo. These general results, the hydrolysis of the fats and proteins, and the formation of sugar, have been observed in all of the work on endosperm metabolism during germination.

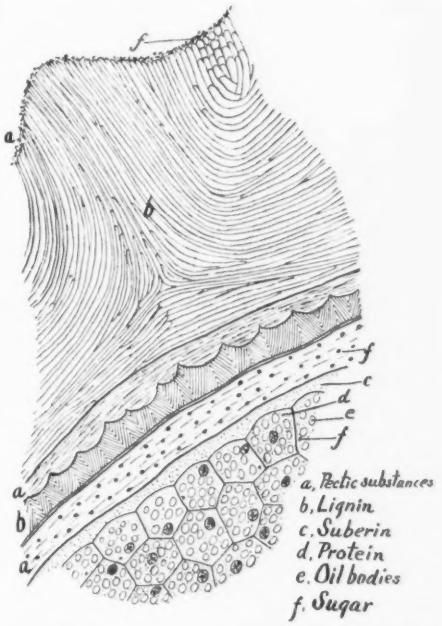

FIG. 3.—Cross-section of pericarp and portion of endosperm: *a*, pectic substances; *b*, lignin; *c*, suberin; *d*, protein; *e*, oil bodies; *f*, sugar.

PERMEABILITY STUDIES.—The seeds absorb water readily, but it was a question whether the water was not all taken up by the woody pericarp, not reaching the embryo at all. Seeds of collection no. 2 were oven dried at 40° C. for six hours and the pericarps

removed. Lots of ten seeds each were weighed carefully and placed in distilled water, in N/10 KOH, and in N/10 HCl. Weighings were made after twelve, twenty-four, and thirty-six hours. After twenty-four hours, lots 1 and 3 lost slightly in weight. The greatest gain was by the seeds in N/10 KOH, which showed a 26.5 per cent increase after thirty-six hours. Although not sufficient data were taken to plot a curve of water intake, yet apparently the rate of intake for *Ilex* seeds agrees in general with what SHULL (**14**) found to hold for the seeds of *Xanthium*, namely, that the rate of absorption is an inverse exponential function of the amount previously absorbed (table II).

TABLE II

SHOWING COMPARATIVE ABSORPTION, IN MG., OF WATER, DILUTE KOH, AND DILUTE KCl BY TEN SEEDS OF COLLECTION NO. 2, WITHOUT PERICARPS

Time	Distilled H_2O	N/10 KOH	N/10 HCl
0	55.8	55.0	56.1
12 hours	60.6	62.6	62.4
24 hours	69.6	69.1	69.2
36 hours	67.0	69.6	68.8
Per cent greatest increase	24.1	26.5	23.3

Tests with LaMotte's standard indicators showed that the H-ions and the OH-ions enter readily. Microchemical tests for the metals indicated that in aqueous solutions they are excluded. Potassium is an exception. As KOH is a solvent for suberin, tests were devised with a view to making the inner coat permeable to chemical forcing agents. This was accomplished for iron and glucose, as will be seen from tables III–VI. In these tables the results recorded refer to the seed proper, and the order of penetration followed throughout is seed coats, endosperm, embryo, and cavity around the embryo. The symbol − means no penetration; o, penetration to an organ; +, general penetration through an organ.

Comparing table III with table IV, it appears that three hours are necessary for N KOH to penetrate all parts of the entire seed, while, with the pericarps removed, the same amount of pene-

tration takes place in ten minutes. Table III shows that in two hours N KOH will penetrate through the embryo. If a one hour treatment of N KOH is followed by N HCl, the embryo

TABLE III

PENETRATION OF VARIOUS CONCENTRATIONS OF KOH SOLUTION INTO IMBIBED SEEDS

Entire seeds	10 minutes	15 minutes	30 minutes	1 hour	2 hours	3 hours	6 hours	12 hours
10 per cent KOH	ooo−	oooo	++++	.....	.....	.....	.....	.....
N KOH	o−−−	oo−−	ooo−	oooo	oo+o	++++	.....	.....
N/10 KOH	−−−−	−−−−	o−−−	oo−−	oo−−	oo−−	oo−−	oo−−

TABLE IV

PENETRATION OF KOH SOLUTIONS INTO SEEDS WITH PERICARPS REMOVED

Collection no. 2	3 minutes	5 minutes	10 minutes	15 minutes
N KOH	+ooo	+o+o	++++	.....
N/10 KOH	+o−−	+ooo	+ooo	+o+o
N/20 KOH	o−−−	+o−−	+o−−	+oo−

TABLE V

PENETRATION OF HCl AFTER TREATMENT WITH KOH INTO ENTIRE SEEDS

1 hour	HCl	15 minutes	30 minutes	1 hour	2 hours	6 hours	12 hours
From KOH 10 per cent	N	o−−−	oo−−	ooo−	oooo	.....	.....
	N/10	−−−−	−−−−	−−−−	o−−−	oo−−	ooo−
	N/100	−−−−	−−−−	−−−−	−−−−	−−−−	−−−−
From KOH N	N	o−−−	ooo−	oo+o	.....	.....	.....
	N/10	−−−−	−−−−	o−−−	o−−−	oo−−	oooo
	N/100	−−−−	−−−−	−−−−	−−−−	o−−−	oooo
From KOH N/10	N	oooo	.....	.....	.....	.....	.....
	N/10	oooo	++++	.....	.....	.....	.....
	N/100	−−−−	−−−−	o−−−	o−−−	o−−−	oo−−

becomes thoroughly acid in one hour. N HCl by itself penetrates more slowly than N KOH.

An aqueous solution of $FeCl_3$ does not penetrate into the endosperm of untreated seeds with pericarps removed, but after five minutes of N/10 KOH a solution of N/200 $FeCl_3$ penetrates

into the endosperm in twelve hours. Table VII shows that while a 5 per cent glucose solution does not penetrate into the endosperm in forty-five minutes, a general penetration to glucose can be secured by a previous treatment of N KOH for a similar length of time.

Both the dry stored seeds and the freshly gathered ones show a P_H value of 6. The seeds that have been imbibed for a year are a little nearer neutral. Seeds of collection no. 2 when treated with

TABLE VI

PENETRATION OF $FeCl_3$ INTO SEEDS WITH PERICARP REMOVED AND TREATED WITH N KOH FIVE MINUTES

Collection no. 2	15 minutes	60 minutes	12 hours
10 per cent $FeCl_3$	o− − −	+o− −	+ooo
N/200 $FeCl_3$	− − − −	o− − −	+o− −

TABLE VII

PENETRATION OF 5 PER CENT GLUCOSE (IN MINUTES) BEFORE AND AFTER TREATMENT WITH N KOH; SEEDS WITH PERICARPS REMOVED

5 per cent glucose	N KOH (minutes)					
	3	5	10	15	30	45
Minutes:						
3	Very slight					
5		Slight				
10			Some			
15				First row of cells		
30					3–4 rows of cells	
45*						General

* 5 per cent glucose does not penetrate in this time.

N KOH showed P_H 10.5 in twenty-four hours; with N HCl the P_H value was 3.5 after the same length of time (tables VIII, IX).

After washing the strongly alkaline and strongly acid seeds for half an hour in distilled water, sections of both embryo and endosperm resisted the entrance of methylene blue solution 1:10,000 for over five minutes. It is evident, therefore, that *Ilex* seeds are very hardy as regards acidity and alkalinity. All of the collections

show vigorous catalase activity. A rough ratio between the oldest seeds and the most rapid growing would be 1:3. This ratio holds for both endosperm and embryo.

FORCING: *A*.—Although none of the simple temperature cultures of entire seeds germinated, yet certain results should be mentioned briefly. The imbibed seeds kept in the icebox for a year responded very slowly to germinating conditions. The best

TABLE VIII

P_H VALUE OF VARIOUS COLLECTIONS OF SEEDS; DETERMINATION AT CENTRAL ENDOSPERM

P_H	Dry	Imbibed	HCl N 12 hours	HCl N 24 hours	KOH N 24 hours	KOH 10 per cent 10 minutes HCl N/10 12 hours
Collection:						
no. 2	7	6.5	.....	.....	.....	.....
no. 3	.....	6	5	3.5	10.5	4.5
no. 5	6.5	6	.....	.....	.....	.....

TABLE IX

P_H VALUE IN DIFFERENT PARTS OF SEED

Collection no. 2	Conc. H_2SO_4 1 hour	Conc. H_2SO_4 2 hours	N/500 HCl 12 hours	N/500 HCl 48 hours	Distilled H_2O
Coats	3–5	3–5	3–5	3–5	6
Endosperm	6	6	6	6	6
Embryo	6	6	6	6	6
Cavity	6.5	6.5	6.5	6.5	6.5

growth occurred at 20° C. The dry stored seeds of nos. 1, 2, and 4 were not accelerated in growth beyond the room controls, except perhaps at −5° C. for no. 2. The fresh berries from no. 5 were influenced favorably by thirty days of low temperature. The evidence is not conclusive as to whether −5° C., 0° C., or 5° C. is the best.

A quantity of berries from no. 2 was agitated mechanically for twenty hours. After sixty days at 25° C. the embryos were considerably larger than those of the controls, probably from the increased permeability due to abrasion. Dry berries from no. 4

and imbibed seeds from no. 2 were kept in the light box for thirty days. They differed from the control in that there was a greater differentiation, but not so much enlargement in the embryos. The attempted electrical stimulation resulted in a depression.

B.—Entire seeds from nos. 2, 3, and 5 were subjected to a variety of chemicals, in approximately 0.1 normal concentration, such as HCl, KOH, $NaHCO_3$, Na_2CO_3, KNO_3, $CaHPO_4$, and acetic acid,

TABLE X

SUMMARY OF CULTURES WITH PERICARPS REMOVED

Culture	Collection	Treatment	Temperature (° C.)	Germination
1	2	Distilled water 30 days, then tap water	30	None
2	2	N/10 HCl 48 hours, washed distilled H_2O	30	None
3	2	N/1000 HCl in quartz flour	25	None
4	3	N/1000 HCl	30	None
5	2	N/10 KOH 48 hours, washed distilled H_2O	30	None
6	2	Imbibed 5° C. 3 months, pericarps removed, N/10 KOH 5 minutes, N/10 HCl 5 minutes	25	None
7	2	N/10 KOH 15 minutes, N/10 HCl 4 minutes	30	None
8	2	N/5000 $ZnSO_4$, N/200 Fe_2Cl_6	30	None
9	3	N/5000 $ZnSO_4$, N/200 Fe_2Cl_6 in quartz flour	30	None
10	2	10% dioxogen in quartz flour	30	None
11	2	N/10 KOH 5 minutes, N/10 HCl 5 minutes, 5% dioxygen 36 hours	30	None
12	2	1% dextrose	30	None
13	2	5% dextrose 2 months, 10° C., pericarps removed	30	40%
14	2	5% dextrose	25	60%
15	2	5% dextrose	30	60%
16	5	5% dextrose 10 weeks 40° C., pericarps removed, N/1000 HCl	30	50%
17	3	5% dextrose	30	None
18	2	Lipase from sprouted sunflower seeds	30	None
19	2	N/50 acetic acid	30	None
20	2	N/500 butyric acid in quartz flour	30	None
21	2	10% dioxogen 6 hours, etherized 12 hours	30	None
22	2	−5° C. 8 days, etherized 24 hours	30	None
23	5	−5° C. 90 days, 10% dioxogen 6 hours, etherized 12 hours	30	None
24	5	Frozen in sand 8 days, etherized 24 hours	30	None
25	5	Sterilized soil from under holly trees	20	None

with no marked results. The use of dioxogen for moistening the seeds worked well for the first thirty days. Knop's solution on the seeds of no. 2 gave negative results. The seeds of nos. 2, 3, and 5 which were treated with 5 per cent solutions of dextrose, levulose, and extract from the holly berries gave decidedly the best results in

size and differentiation of the embryos. None of the 130 cultures with entire berries or cleaned seeds was successful after twelve months of observation.

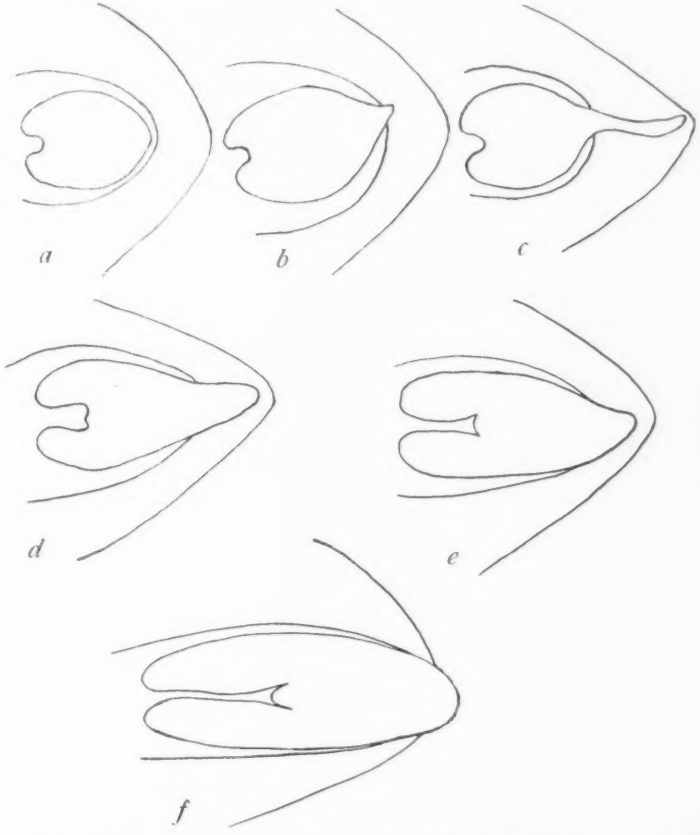

FIG. 4.—Selected stages from culture 14 of table X: *a*, July 14, 1921; *b*, July 28, 1921; *c*, August 19, 1921; *d*, October 16, 1921; *e*, December 8, 1921; *f*, January 13, 1921; camera lucida ×100.

In selecting the chemical forcing agents and determining the proper concentration to use with the seeds without pericarps, the papers of JENSEN (9) and of Miss ECKERSON were consulted. Table X gives a summary of the cultures with pericarps removed.

Although the negative results in table X are expressed as "germination none," yet it should be noted that considerable variation occurred. For instance, in culture 9 with collection no. 3, all the seeds became infected and decayed within a week, and in culture 24 with collection no. 5 some of the seeds survived over eleven months. All of the cultures were moistened with distilled water for the first thirty days, but after they were transferred to Birmingham

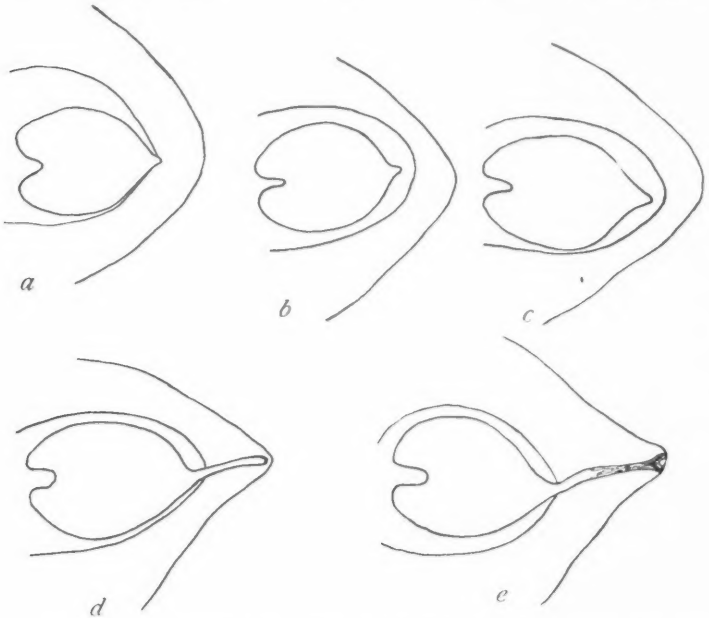

FIG. 5.—Selected stages from culture of collection no. 4 with cleaned seeds kept at germinating conditions for twelve months: *a*, April 8, 1921; *b*, June 4, 1921; *c*, June 26, 1921; *d*, July 28, 1921; *e*, April 11, 1922; camera lucida ×100.

it was found, by experimentation, that ordinary tap water does as well if not better than distilled water. For approximately four months tap water was used exclusively to keep the substratum moistened.

Contrasting stages of seeds which germinated and those which did not are illustrated by fig. 4 (*a–f*) and fig. 5 (*a–e*). The divided hypocotyl tip shown in fig. 5*e* is an extreme case. Usually in the

seeds with intact pericarps the filamentous hypocotyl just comes to the surface of the endosperm and dies.

Most of the cultures with pericarps removed show more growth in one month than those with entire seeds do in five months. The cultures treated with glucose germinated after five months in ovens at temperatures from 25°–30° C. The hypocotyls broke through the seed coats and the embryos had grown to one-third the length of the endosperms with well formed cotyledons and organized plumules. The freshly gathered seeds and the one-year dry stored seeds germinate equally well.

Discussion

Ilex opaca is found sparsely distributed throughout the moist woodlands of the southern United States. Only in small areas does it ever become a dominant forest form. The ratio of germination in nature, under favorable conditions, is not over 1:1,000,000, while the average for the range probably would be about 1:10,000,000.

The causes for this low percentage of germination are to be found in (1) the pericarp, (2) the embryo, and (3) the water supply. The pericarp of the holly is peculiarly unfavorable to germination, in that it not only has a tough woody structure (fig. 3) but it has no natural lines of dehiscence. The decay of the pericarp furnishes the only means of escape for the embryo. The pericarp does not become sufficiently weakened by decay to allow the protrusion of the hypocotyl until the second year in the ground. By this time, however, the embryo is usually dead. A very close co-ordination of natural conditions must prevail in order that the embryo development may be retarded and the pericarp decay hastened to such an extent that the former is ready to emerge just as the latter is about to disintegrate. The seasonal distribution of the rainfall is an important factor in the natural germination. Two or three months of successive dryness in the summer or fall would not be injurious, while two or three weeks without rain in the late winter or spring probably would be fatal to germination.

The embryo of *Ilex* is in a very immature condition (fig. 1) when the berry falls from the tree. At the time the berries turn

red in December, the embryo is nothing more than a spherical mass of tissue. From then until the berries are shed there is a gradual differentiation, which only amounts at the most to a slight elongation and the formation of rudimentary cotyledons. At any time during the spring the embryo will respond to the proper germinating conditions and grow continuously, although slowly, until the hypocotyl breaks through the seed coats. The embryo, therefore, is never dormant, nor does it require a period of after-ripening. The embryo, however, does have a long period (8–12 months) of very slow growth. Comparisons of figs. 4 and 5, made at appropriate intervals, will show conclusively that embryo development is continuous. Growth, more or less rapid, is manifest under a wide range of conditions, as for example at temperatures from 0° to 30° C., in the presence of mineral acids, bases, and salts in concentrations from N/5000 to N/10, and of organic acids and sugars.

This immaturity of the embryo constitutes the main factor in the delayed germination. Another factor equally significant in producing delay, although more capable of modification, is the inability of the embryo to penetrate the intact pericarp. Of the 130 cultures of entire seeds kept under observation from eight to twelve months, not a single seed was able to overcome this barrier. In many instances slender hypocotyls grew through the endosperm, but eventually died (fig. 5*e*) because they were unable to grow more than 3–4 cells in diameter. Since the pericarp is easily penetrated by water and by chemical forcing agents, the delay is not brought about by the exclusion of water. The freeing of the endosperm with its inclosed embryo from the mechanical restraint of the woody pericarp, therefore, constitutes a necessary condition for successful germination.

The conditions under which the embryo will germinate are:

1. A continuous temperature of 25°–30° C. This does not mean that lower temperatures, even −5° C. for thirty days, will not be successful, but simply that the best results are to be obtained by using these temperatures.

2. A substratum kept continuously moist with tap water rather than with distilled water. It is especially important that the cul-

tures should not dry out completely during the last few weeks of embryo development.

3. The removal of the pericarp. The concentrated H_2SO_4 method of treatment of hard coated seeds is not adapted to *Ilex* because of the irregularities in the surface of the nutlets. The method adopted, of oven drying and then cutting away, is effective in securing uninjured endosperms and embryos, but is not a suitable method for commercial propagation on account of its slowness.

4. A treatment with 5 per cent dextrose. This is the only successful forcing agent discovered (see table X), and it is significant that dextrose is the main ingredient of the berry pulp. It is probable that the sugar of the berry serves a threefold purpose, to prevent too great desiccation, to promote pericarp decay, and to feed the embryo. The importance of sugars in the germination of minute embryos has been recognized by KNUDSON (**10**) in his work with orchid seeds. Here there is no endosperm, and the embryos require greater protection than the *Ilex* seeds. It should be noted as a further evidence of the importance of glucose as a forcing agent, that it was effective on all the seeds where it was used, regardless of the previous treatment of the seeds. The successful germinations reported in table X were in cultures that differed widely in the preceding treatment of the seeds. The only condition common to the successful tests is the presence of glucose. Some of the seeds used were from air dried berries a year old, others had just been gathered from the tree. One culture had been kept imbibed for sixty days at 10° C., then dried, the pericarps cut away, and the endosperms with inclosed embryos placed in germinating conditions. Another culture had been uninterruptedly at 30° C. All of these were forced to about the same degree by the presence of the 5 per cent glucose.

5. An increased permeability of the seed coats is highly desirable. As found by GOLA (**8**) and SHULL (**14**), semipermeability of seed coats is a widespread phenomenon, but not all seeds possessing such coats exhibit semipermeability to the same degree, nor to the same solutes, nor is the selective property always resident in the same layers. In the case of the holly the suberized layer next to the endosperm is mainly responsible for the exclusion of dextrose in

solution, but a treatment, modified from tables IV, V and VII, of the seeds with N KOH for five minutes and then with N HCl for three minutes will render them easily penetrable. Only very small quantities of sugar were ever found in the untreated endosperms, which shows that the embryos use it up almost as fast as it is available. The growth of the embryo seems to be rather closely limited by the amount of sugar which it can obtain, provided, of course, that the other conditions for development are favorable. The treatment with dilute KOH, therefore, by changing the permeability of the suberized portions of the seed coat, makes it possible to supply the embryo with necessary food much more rapidly than occurs by the slow hydrolysis of the stored fats of the endosperm.

Summary

1. Germination of seeds of *Ilex* in nature requires from one to three years, and the percentage of germination is about one in ten million.

2. Natural germination is not confined to hydrophytic conditions, as has usually been claimed, but occurs as well in mesophytic situations.

3. Stratification of the seeds is unnecessary.

4. There is no after-ripening.

5. Germination is impossible with pericarps intact.

6. The pericarps can be removed by drying the seeds for six hours in the oven at 40° C. and then cutting away.

7. A 5 per cent solution of dextrose is an efficient forcing agent.

8. The permeability of the seed coats to sugar can be increased by treating with dilute KOH solutions, which act upon the suberized tegmen.

9. A sugary substratum kept moist with tap water produced hypocotyl protrusion in about five months.

Grateful acknowledgment is made to Dr. WILLIAM CROCKER, under whose direction the greater part of the investigation was conducted, to Dr. SOPHIA H. ECKERSON for valuable suggestions in connection with the microchemical studies, and to Dr. CHAS. A. SHULL for helpful criticisms of the work and the manuscript.

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NEW OR OTHERWISE NOTEWORTHY COMPOSITAE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 309

EARL EDWARD SHERFF

(WITH PLATES VI–IX)

Isostigma glycinaefolium (Schz. Bip. ex Baker), comb. nov.; *Bidens glycinaefolia* Schz. Bip. ex Baker, in Mart. Fl. Bras. 6[III]:247. 1884. Pl. VI.

This species is very rare in herbaria. It was described as a *Bidens* by BAKER (*loc. cit.*) from RIEDEL's specimen in Kew, with the geographic note: "Hab. in campis Brasiliae, loco non adnotato: RIEDEL!" The Schultz Bipontinus Herbarium (now in Herb. Mus. Hist. Nat., Paris) contains a specimen bearing RIEDEL's original field data: "In subhumidis graminosis.—pr. Cuyabá. Maio 1827. Brasilia." Both of these specimens have mature achenes but lack flowering heads. Their crowded alternate leaves, frequently erose-margined exterior involucral bracts, and four-toothed disc florets form, however, a combination of characters anomalous in *Bidens*. Recently I have found among the specimens in the Herbarium of the Botanical Museum of Berlin two more specimens from the same locality: *R. Pilger* 479, scattered upon stony ground at the foot of the Serra das Pedras in Cuyabá Valley, Mättogrosso, Brazil, April 15, 1899, two sheets. The several flowering heads present show at once that the species belongs to *Isostigma*, a genus founded upon four other Brazilian species by LESSING in 1831 (Linnaea 6:513). The following amplified description is drawn up from all four specimens examined, but the illustration is mainly from the specimen of SCHULTZ BIPONTINUS' private herbarium.

ISOSTIGMA GLYCINAEFOLIUM, descript. amplif.[1]—Herbacea, perennis, glabra, ±6 dm. alta; caule simplici nisi versus apicem, subtereti, inconspicue angulato, supra subnudo, infra dense folioso, e basi ligneo. Folia glaucescentia (ex RIEDEL), eis graminearum valde similia, sessilia, inferiora 8–19 cm. longa et 4–10 mm. lata, conferta, superiora sensim minora et distantia, omnia alterna vel perpauca opposita, indivisa, linearia, elongata, apice acuminata, infra

[1] The name was distinctly spelled "*Bidens glyceriaefolia*" by SCHULTZ BIPONTINUS, both on the label and on the packet in his herbarium, although later published by BAKER as spelled here.

angustata, basi ipsa plerumque dilatata atque amplexicaulia, integra vel parce antico-serrata dentibus angustis acribusque, rigidula et parce membranacea, margine non ciliata. Capitula perpauca (circ. 4–9), laxe corymbosa, pedunculata pedunculis 3–14 cm. longis, radiata; ligulis circ. 10–12, flavis, linearibus, apice bidentatis, 9–13 mm. longis; paleis versus apicem perspicue longo-attenuatis; disci floribus ad apicem acriter 4-dentatis; disco demum circ. 12 mm. lato ac 6–9 mm. alto. Involucrum glabratum sed minutissime tuberculo-rugulosum, bracteis rigidulis, adpressis, lanceolatis, margine saepe erosis, exterioribus 3–5, acutis, 4–5 mm. longis; interioribus ad apicem saepe attenuatis, paulo longioribus. Achaenia (submatura) anguste lineari-cuneata, compresso-tetragona vel demum subtetragona, rubro-nigrescentia, exalata, marginibus ac costis medianis suberecte setosa, alibi glabra, corpore 5–8mm. longa, biaristata; aristis tenuibus, calvis vel versus basim arrecte setulosis (vel omnino rigide ciliatis ex BAKER), 1–2 mm. longis.

Bidens Holstii (O. Hoffm.), comb. nov.; *Coreopsis Holstii* O. Hoffm. in Engler Pflanzenw. D. Ost Afr. C: 415. 1899.

HOFFMANN'S type in Berlin consists of three flowering specimens mounted upon one sheet. They completely lack mature or even submature achenes. At first they had been determined by him as *Coreopsis Grantii* Oliv. (*Bidens Grantii* Sherff), but later he had crossed out this determination and substituted the new name *C. Holstii*. His description of the achenes ("achaeniis juvenilibus alatis") was of necessity drawn from the unripened ovaries. The winged character assigned by him to the young achenes is not manifest on my examination of them. They naturally are thin and delicate toward the edges, but this is true of the achenes of many typical *Bidens* species when equally young. Fortunately there have been collected since and deposited in the Herbarium of the Botanical Museum of Berlin three additional specimens from the type district, Usambara: *Braun* 2820 and 2857, Kingo-Kwai, West Usambara, August 21, 1909; "N.Z." 1776, Hermannsplatte, February, 1908. These match the type very closely, and two excel it in having mature achenes. The achenes are linear, unwinged, 3–6 mm. long, flattened, upwardly setose upon the margins and at the apex, exaristate or with two setae very slightly larger than the rest and representing minute aristae (cf. Hoffm., *loc. cit.*, "aristis 2 brevissimis"). The species bears a strong habital resemblance to *Bidens Grantii* (Oliv.) Sherff, and in less degree to *Coreopsis pinnatipartita* O. Hoffm. From the latter it differs in its setose, exalate achenes; from the former it appears to differ mainly in having the achenes exaristate, a character here of somewhat uncertain value.

Coreopsis oblonga, sp. nov. (pl. VII)—Herba erecta, verisimiliter perennis ac 6–12 dm. alta; caule obtuse tetragono, atro, versus apicem pubescenti, alibi glabro. Folia petiolata petiolo hispido-ciliato vel brevi (usque ad 1.5 cm. longo) latoque vel longiore (usque ad 3 cm.) et parce angusto, petiolo adjecto 6–7.5 cm. longa, rigida et subcarnosa, pinnata, foliolis acriter dentatis dentibus calloso-apiculatis, subprofunde incisis sinibus angustis vel foliolis lateralibus infimis etiam tripartitis, breviter hispido-ciliatis, setis acribus sparsissime vestitis, terminali oblongo-lanceolato, lateralibus oblongo-ovatis. Capitula pauca, breviter pedunculata pedunculis subrobustis ac hic illic foliolo-bracteatis usque ad 6 cm. longis, radiata, ad anthesin 2.5–3 cm. lata et 9–11 cm. alta. Involucrum setis validis acribusque hispidum; bracteis exterioribus 6–9, late lineari-spathulatis, versus apicem glabratis, apice subobtusis, 8–11 mm. longis, eis capitum juniorum discum manifeste superantibus; interioribus oblongo-oblanceolatis vel oblongo-obovatis, versus apicem constricta, exterioribus demum subaequalibus. Flores ligulati ±7, aurantiaci, ligula elliptico-lanceolati, apice late obtusi et integri denticulative, circ. 15 striis percursi, tubo adjecto 1.5–2.4 cm. longi, tubo circ. 5 mm. longo; flores tubulosi infundibuliformes, limbo aurantiaci, 5-lobati, facie exteriore striis nigris 5 conspicue percursi, infra pilosi (ad medium etiam longe hirsuti), supra perpaucis pilis interdum conspersi. Achaenia matura non visa. Ovaria subnigra, oblongo-cuneata, alata, plana, faciebus glabra, corpore 2–3 mm. longa et 0.7–1 mm. lata, apice arrecte setosa et longe biaristata; aristis acribus, supra et ad medium glabris, versus basim setulis arrectis 1–3 sparsim munitis, 2–2.5 mm. longis.

Alex. Carson 106, Lake Tanganyika, East Equatorial Africa, September 1893 (type in Herb. Kew).

A species approaching *Coreopsis pinnatipartita* O. Hoffm., *Bidens Grantii* (Oliv.) Sherff, and *B. Holstii* (O. Hoffm.) Sherff. The hairy, aristate ovaries distinguish it easily from *C. pinnatipartita*, while the definite wings of the ovaries distinguish it from *B. Grantii* and *B. Holstii*.

HETEROSPERMUM RHOMBIFOLIUM (Schz. Bip.) Griseb., Goett. Abhand. **19**:138. 1874; *Bidens* (*Heterospermum*) *rhombifolia* Schz. Bip., Bonplandia **4**:54. 1856 (nomen). Pl. VIII.

SCHULTZ BIPONTINUS, who reduced *Heterospermum* to *Bidens*, advanced without description the name *Bidens* (*Heterospermum*) *rhombifolia* for a plant collected by W. LECHLER, no. 1576, at Tana, northern Chile,[2] in rubbish-covered places, May 1854. Later, GRISEBACH (*loc. cit.*) transferred the species to *Heterospermum*, supplying a very scant description: "Species parum ab *H. maritimo* Kth. foliis latioribus (2″ longis, 1″ latis) recedens."

The leaves of *H. maritimum* were described as 4–4.5 lines wide, those of *H. rhombifolium* are 7–9.3 lines wide, and because of this greater width have a remarkably different aspect. The achenes of the outer perfect (hermaphrodite) florets in *H. maritimum* were described as obsoletely tridentate at the apex, but the corresponding achenes of *H. rhombifolium* are definitely biaristate.[3] In 1914, on finding one of LECHLER's original specimens in Paris (Herb. Mus. Hist. Nat.), I made a drawing of it (pl. VIII). The leaves suggested strongly the possibility of the plant's being the "*Heterosperma ovatifolia*" of CAVANILLES, described from "Peru" in 1822 (Cav. Descrip. 204. 1802), and later definitely named *H. ovatum* by WILLDENOW (Sp. Pl. ed. IV. **3**:2129. 1804).[4] CAVANILLES' description of the leaves, however, "Las hojas son aovados, de cinco á ocho lineas de largo," shows his plant to have been one of the smaller-leaved species native to that region. In the Paris specimen of *H. rhombifolium* the principal leaves all measure from 9 to 16 lines long,[5] not 5–8 lines as given by CAVANILLES. The plant, on comparison with KUNTH's plate in HUMBOLDT and BONPLAND *Nova Genera et Species Plantarum* (**4**: *pl. 383.* 1820), appears to differ from *H. maritimum* mainly in having large rhombic-ovate instead of small rhombic-lanceolate leaves.

Since the paucity of material in the larger herbaria makes it impossible actually to settle the separate identity of *H. rhombifolium* as distinct from *H. maritimum*, attempts at synonymizing the two would seem to be valueless for the present. As an aid to the future solution of the problem, however, the following description was drawn up from the plant shown in my plate, supplemented by a duplicate specimen in the Herbarium of the Botanical Museum of Berlin.

HETEROSPERMUM RHOMBIFOLIUM (Schz. Bip.) Griseb., descript. amplif.—Herba annua, adscendenti-erecta e basi librata; caule

[2] Taena, Peru, is the locality given on the label.

[3] It should be remarked, however, that in the type plate, fig. 3, of *H. maritimum*, two definite aristae are shown on the achene. No tridentate character is indicated.

[4] In CAVANILLES' description, the name "*Heterosperma ovatifolia*" appears (according to Miss MARY A. DAY of Gray Herbarium, who has kindly furnished me a written copy) not as a binomial but merely as the first two words of a short Latin description, followed by a longer Spanish description. WILLDENOW's citation of CAVANILLES' plant is definite and makes it the type of *Heterospermum ovatum* Willd.

[5] GRISEBACH's measurements, "2″ longis, 1″ latis," appear to have been carelessly taken.

ramisque dichotomis, pilosis. Folia opposita, membranacea, parce alato-petiolata, rhomboideo-ovata, 2–3 cm. longa, dimidio inferiore subcuneato integra, circum dimidium superius (duobus marginibus inclusis) 7–9-dentata, ad basim hispido-ciliata, aliter glabra. Pedunculi singulatim inter ramos duos dispositi. Capitula ad anthesin circ. 5–6 mm. alta et circ. 5 mm. lata, in fructu 1–1.4 cm. alta et 7–10 mm. lata. Involucri bracteae aequilongae; exteriores margine pilis multiloculatis ciliatae, aliter glabrae, inferne angustae, superne latiores, apice acutae et indurato-apiculatae, 5–7 mm. longae. Flores ligulati circ. 4, feminei, flavi, subglabri, ligula obovati, apice acute tridentati, erecti, plani, subsexnervii, vix exserti, tubo (circ. 1.5 mm. longo) adjecto circ. 2.5–3 mm. longi. Achaenia compressa extrema (florum femineorum) late oblanceolata, exaristata, glabra, corpore atra, alata alis brunneis inferne sensim sed superne magis abrupte angustata, circ. 5.5–7 mm. longa et circ. 2 mm. lata; interiora late vel anguste linearia, margine alato sursum plus minusve hispida, biaristata aristis retrorsum hamosis at 2–3.5 mm. longis, corpore 7–8.5 mm. longa et 1.5–2 mm. lata; intima angustiora, facie minute papillata et magis perspicue striata, exalata, supra etiam faciebus sursum hispida, corpore 7–9 mm. longa et 0.8–1.2 mm. lata, biaristata aristis retrorsum hamosis 2.5–3.5 mm. longis.

Bidens Steppia, comb. nov.; *Corcopsis Steppia* Steetz in Peters Nat. Reise nach Mossambique 496. 1862–64.

The type material of *Bidens Steppia* was collected by Dr. WILHELM PETERS, no. 57 ("an verschiedenen Orten nahe feuchten Stellen," ex herb. inscript.), Rios de Sena, Mozambique, Africa, 1842–48.[6] The two type specimens are still extant in fairly good condition (Herb. Berl.). Their several mature achenes are seen on close inspection to be devoid of true wings (cf. PETERS, *loc. cit.*, "achaeniis oblongis subcompressis marginatis sed vix alatis"), and to have merely rough, thickened margins, similar to those on certain species of true *Bidens*, *ex. gr.*, *B. aristosa* (Michx.) Britton. In a previous paper[7] I have shown the reasons for regarding such plants as belonging to *Bidens*.

[6] I have been supplied with STEETZ's original Latin description by Miss MARY A. DAY, Librarian at Gray Herbarium, whose kindness is here gratefully acknowledged. An essentially similar description is given in English by OLIVER (Fl. Trop. Afr. **3**:388. 1877), who probably had seen the type specimens, as he correctly applied this name to two other specimens in Kew Herbarium (by MELLER and by KIRK).

[7] BOT. GAZ. **59**:305–308. 1915.

A study of herbarium material reveals several specimens that match those of the type: *Antunes* 197, Huilla, Portuguese West Africa (Herb. Berl.); *Braun* 5505, growing 1 m. high, Niamutukusja-Nsera, Prov. Bukoba, German East Africa, June 15, 1913 (Herb. Berl.)[8]; *J. Buchanan* 251, Nyassaland in 1891 (Herb. Berl., two sheets); *K. J. Cameron* 38, Namasi, commun. December 19, 1899 (Herb. Kew); *John Gossweiler* 1203, Malange, Angola, in 1903 (Herb. Berl.); *Kirk*, alt. 3000 feet, Maganja Hills, Zambesi-land, commun. February 1866 (Herb. Kew); *C. J. Meller*, about latitude 16°S., longitude 35°E. (thus vicin. Blantyre, Nyassaland), August-September 1861 (Herb. Kew); *Ad. Stolz* 729, growing 1.5 m. high at alt. of 1350 m., Kyimbila, Kaningwe, Langenburg, German East Africa, May 26, 1911 (Herb. Berl.); *Stuhlmann* 2120, alt. 1500 m., Ruhanga, Mpororo (Uganda), August 20, 1891 (Herb. Berl.); anonymous, "no. 119," Mozambique, 1884–85 (Herb. Berl.).

Coreopsis Mattfeldii, sp. nov.—Herba erecta, ramosa, verisimiliter circ. 7–10 dm. alta, caule subtetragono, glabrato vel disperse piloso, sulcato. Folia petiolata petiolis latis ± 1 cm. longis, petiolis adjectis 4–10 cm. longa, pinnatisecta, utrinque moderatim pilosa, margine parce ciliata, laciniis oppositis indivisis vel pinnatisectis, segmentis ultimis linearibus (2–4 mm. latis), acutis atque induratoapiculatis. Capitula corymbosa, radiata, pansa circ. 3.5 cm. lata et 9 mm. alta, ligulis circ. 8, flavis, lanceolatis vel obovatolanceolatis, striatis, apice obscure minuteque denticulatis, 1.6–2 cm. longis et 4–9 mm. latis. Involucri bracteae dorso hispidae pilis albis multiloculatis atque ad basim tumidis, aequilongae (5–8 mm.), exteriores lineari-spathulatae, interiores ovato-lanceolatae. Achaenia valde compressa, nigrescentia, alata alis 1–1.5 mm. latis, faciebus glabra vel ad costas (et supra sparsim) hispida, margine apiceque hispida, biaristata aristis tenuibus sursum hispidis 1–2 mm. longis, exteriora obovata 6–8 mm. longa et 4.25–5 mm. lata, interiora oblanceolata circ. 8 mm. longa et 4 mm. lata.

Carson 75, Fwamba, German East Africa, in 1894 (type ex Herb. Kew in Herb. Berl.).

Recently, among the large collections of *Bidens* and *Coreopsis* in the Herbarium of the Botanical Museum at Berlin, a number of specimens, chiefly from Africa, were found to represent undescribed species. The one given here is named very appropriately after Dr. JOHANNES MATTFELD, who most generously

[8] *Braun* 5505 and *Stolz* 729 are tall plants 1–1.5 m. high, with achenes having body 6–9 mm. long and only 1–1.25 mm. wide. They are connected, however, with the type of *B. Steppia* (having achenes 7.5–9 mm. long and 2.5–3 mm. wide) by various intergradations, and do not appear deserving of separate specific rank.

placed these many specimens at my disposal for detailed study. It bears a strong superficial resemblance to *Bidens Steppia*, but can easily be distinguished by its achenes and involucral bracts. The many mature achenes on the type differ remarkably from the ones on the type and other specimens (already cited) of *Bidens Steppia*. For *B. Steppia* they are at most widely oblong-linear in outline, 7.5–9 mm. long and 2.5–3 mm. wide; there is merely a thickened lateral ridge, wings being absent. For *Coreopsis Mattfeldii* the achenes are much thinner and wider, the outer ones being obovate, 6–8 mm. long and 4.25–5 mm. wide, the inner ones being oblanceolate, about 8 mm. long and 4mm. wide; all are winged, and even on submature fruiting heads the rounded upper ends of the wings, adjacent to the aristae, are easily visible to the eye. The external bracts about equal the inner ones in *C. Mattfeldii;* in *Bidens Steppia* they tend to exceed the inner ones by 2–6 mm.

Bidens microcarpa, nom. nov.; *Coreopsis exaristata* O. Hoffm. in Engler Pflanzenw. Ost Afr. C: 414. 1895.

Bidens gracilior (O. Hoffm.), comb. nov.; *Coreopsis exaristata* var. *gracilior* O. Hoffm., *loc. cit.*

The type and other specimens cited by HOFFMANN for his *Coreopsis exaristata* and variety *gracilior* have tiny, rough, unwinged and unawned achenes. They are referable to *Bidens* rather than *Coreopsis* (cf. SHERFF, BOT. GAZ. **59**:305–308. 1915).

Bidens lineata, sp. nov.—Herba gracilis, forsan perennis, verisimiliter 5–7 dm. alta; caule moderatim ramoso, subtetragono, sulcato, breviter setoso, internodiis quam foliis plerumque multo longioribus. Folia subsessilia vel breviter petiolata petiolis 2–6 mm. longis, petiolo adjecto 1–4 cm. longa, pinnata, foliolis 3 vel 5, dentatis vel pinnatisectis, lobis linearibus vel lanceolatis, ciliatis et ad costas setosis, aliter hispidis vel etiam fere glabratis, apice plerumque acriter indurato-apiculatis. Capitula radiata, pauca, singulatim fines ramorum terminantia, pansa circ. 3–3.5 cm. lata et 7–8 mm. alta; pedunculis tenuibus 7–15 cm. longis. Involucri bracteae subaequales, 4–7 mm. longae, dorso hispidae, exteriores late lineares, supra saepe latiores, apice obtusae. Flores ligulati 6–8, flavi, elliptico-oblanceolati, apice minute et obscure denticulati, 1.2–1.6 cm. longi. Achaenia nigra, lineari-clavata, tumido-compressa, faciebus 8-sulcata, marginibus et supra inter sulcis sursum hispida vel tuberculato-hispida, corpore circ. 5 mm. longa et 1.2–1.5 mm. lata, tenuiter biaristata aristis lineatis vel lineis rectis valde similibus, retrorsum hamosis, circ. 2 mm. longis.

Dr. R. Endlich 117, at altitude of 1500 m., in summer of 1909, Kilimanjaro, German East Africa (type in Herb. Berl.).

The type specimen had been determined at Berlin as *Coreopsis exaristata* O. Hoffm. (*Bidens microcarpa* Sherff), to which it does indeed bear a strong resemblance. The characters of the involucre and of the aristate achenes, however, are very distinct.

Bidens leptolepis, sp. nov. (pl. IX, figs. *a*–*g*).—Herba annua, erecta, fere glabra, caule angulato, supra ramoso, +4 dm. alto. Folia petiolata petiolis 1–2 cm. longis, petiolo adjecto 4.5–8 cm. longa, pinnatim 3–5 (rariter 7)—partita, foliolis linearibus, membranaceis, acriter apiculatis, marginibus parce ciliatis sed saepe involutis vel revolutis, lateralibus plus minusve prorsum spectantibus, 1–2 mm. latis. Capitula ramos terminantia, pedunculata pedunculis 2–3 cm. (supra bracteam foliosam linearem) longis, radiata, pansa ad anthesin 2.5–3 cm. lata et circ. 7–8 mm. alta. Involucri bracteae valde dimorphae, exteriores 11–15, angustissime elongato-lineares, acriter apiculatae, sparsim ciliatae, basi moderate dilatatae et saepe hispidae, circ. 8 mm. longae et ad medium tantum 0.3–0.5 mm. latae, quam interiores lanceolatae dimidio longiores. Flores ligulati circ. 7, in sicco dense atro-purpurei vel atro-rubri, ligula oblanceolati, apice minute denticulati, 1.2–1.5 cm. longi. Achaenia matura non visa; immatura lineari-oblanceolata vel lineari-oblonga, plana, faciebus glabra, marginibus plus minusve ciliata, corpore circ. 1.5 mm. longa at 0.5 mm. lata, biaristata aristis retrorsum hamosis, circ. 1 mm. longis.

T. Kassner 2725, under trees, Mt. Kundelungu, Congo Free State, May 10, 1908 (type in Herb. Berl.).

Appears closest in foliage and general habit to *Bidens urceolata* DeWild., a species also collected by KASSNER (no. 2710) on Mt. Kundelungu.[9] *B. leptolepis*, however, has smaller flowering heads, very dark red or dark purple, not light violet ligules, much more slender and elongate external involucral bracts, ordinary (not conspicuously margined above) internal involucral bracts, and lacks a definitely urceolate shape to the tubular florets.

Coreopsis Neumannii, sp. nov.—Herba nunc 10 cm. alta, nunc 1.5 m. (forsan etiam ultra) alta, caule maximam partem glabro,

[9] The type of *B. urceolata* came from Lukafu, a station in the same region. I was permitted to examine it through the courtesy of Dr. EM. DEWILDEMAN, of the Jardin Botanique de l'Etat, at Brussels.

sulcato, ramoso, internodiis folia facile superantibus. Folia subsessilia vel petiolata petiolo usque ad 1 cm. longo, petiolo adjecto 2–4 cm. longa, plerumque tripartita (inferiora non visa, pinnata?) foliolis ovatis vel interdum lanceolatis, dentatis vel lobulatis, pubescentibus, dentibus acerrime apiculatis. Capitula corymbosa, 5–11 in singulis corymbis, radiata, pansa ad anthesin 2.2–2.7 cm. lata et circ. 6 mm. alta, pedunculis tenuibus plerumque 1–3 cm. longis. Involucrum inconspicue hispidum, bracteis exterioribus circ. 8, flavido-viridibus, lineari-spathulatis, apice acutis, 3–7 mm. longis, quam interioribus lanceolatis paulo brevioribus. Flores ligulati plerumque 8, flavi, ligula elliptico-oblongi, paucistriati, apice integri vel denticulati, circ. 1.2 cm. longi. Achaenia plumbeo-nigra, circumambitu lineari-oblonga vel oblanceolata, valde compressa, alata alis coloris similis, glabra, corpore 3–4 mm. longa et (alis inclusis) 1.0–1.5 mm. lata, biaristata aristis brevissime sursumque setosis, circ. 0.5–1 mm. longis.

Oscar Neumann (Exped. to Sidamo, Utadera, and Lake Abbaja) 134, mountain meadows at altitude of 2800 m., Gandulla, eastern Africa, January 14, 1901 (type in Herb. Berl.).

The single type specimen has its heads in corymbose clusters, and thus simulates in habit *Bidens squarrosa* H.B.K. of America.

Coreopsis scabrifolia, sp. nov.—Herba simplex vel parce ramosa, caule quadrangulato, glabro, sulcato, perenni e basi lignea, verisimiliter circ. 1 m. alto, non robusto. Folia nunc sessilia, nunc petiolata petiolis alatis et elongatis usque ad 4 cm. longis, petiolo adjecto 8–15 cm. longa et 1–3 cm. lata, lanceolata, indivisa, acriter et interdum grosse dentata, utrinque acuminata vel tantum acuta, scabra, minute spinuloso-ciliata, infra ad venas sparsim piloso-hispida et pallidiora. Capitula pauca (1–4), subtenuiter pedunculata pedunculis per maximam partem glabris 3–12 cm. longis, radiata, pansa ad anthesin 5–6 cm. lata et circ. 1 cm. alta. Involucri bracteae exteriores 8–11, lineares vel lineari-lanceolatae, dorso basi hispidae, 1–1.5 cm. longae, interiores lanceolatas aequantes vel paulo superantes. Flores ligulati circ. 8, flavi, ligula elliptici vel ovato-lanceolati, 2–2.5 cm. longi et 5–12 mm. lati. Achaenia brunneo-atra, late linearia, valde compressa, moderatim sed inconspicue alata, sursum setosa, corpore 9–11 mm. longa et (alis inclusis)

2–3 mm. lata, biaristata, aristis nudis vel sursum 1–3-spinulosis, 1.5–2.5 mm. longis.

T. Kassner 2776, under trees, Kundelungu, Congo Free State, May 15, 1908 (type in Herb. Berl.; two co-type sheets in Herb. Brit. Mus.).

In a determination of plants from the Congo Free State, DEWILDEMAN (Ann. Mus. Congo, Bot. Ser. IV. 2:169. 1913) refers this plant to *Coreopsis guineensis* Oliv. and Hiern., but the true *C. guineensis* is a very different plant. The general habit of *C. scabrifolia* is deceivingly like that of *Bidens Baumii* (O. Hoffm.) Sherff, and were it not for the sharp achenial and involucral differences, distinction between the two would be at times very difficult.

Coreopsis togensis, sp. nov.—Herba magna, probabiliter perennis; caule glabro, rubro-viridi, sulcato, subtetragono, usque ad 2 m. alto. Folia petiolata petiolis 0.5–4 cm. longis, petiolo adjecto 10–18 cm. longa et usque ad 20 cm. lata, pinnatim 3- vel 5- partita, foliolis lanceolatis, apice saepe longe attenuatis, grosse vel moderatim serratis dentibus acriter apiculatis infra pallidioribus, margine minute ciliatis, aliter glabris, lateralibus usque ad 11 cm. longis et 3 cm. latis, terminali usque ad 16 cm. longo et 4 cm. lato. Capitula pauca, longe pedunculata pedunculis maximam partem glabris usque ad 18 cm. longis, radiata, pansa ad anthesin 7–9 cm. latis et circ. 1.5 cm. alta. Involucrum non plerumque pubescens nisi basi, bracteis exterioribus 7–10, magnis, foliaceis, lanceolatis, apice angustatis, interdum ciliatis, 1–2 (et etiam usque ad 4) cm. longis, interiores lanceolatas aequantibus, vel multo superantibus. Flores ligulati 7–9, lutei, ligula late elliptico-lineares vel ovato-oblanceolati, apice minute vel grosse profundeque (sinu usque ad 1 cm. alto) dentati, 3–4.5 cm. longi et 0.7–2 cm. lati. Achaenia compressa, brunneo-atra, oblongo-linearia, plerumque alata, margine sursum ciliata, supra faciebus et apice erecto-hispida, corpore 8–10 mm. longa et (alis inclusis) 2.5–3 mm. latis, biaristata aristis nudis vel versus basim sursum 1- vel 2- spinulosis, circ. 1 mm. longis.

Dr. R. Buettner 142, on steppe behind Ketzabenki, Togo, August 29, 1890 (two type sheets in Herb. Berl.); *Dr. W. Busse* 3416, at altitude of about 700 m., Hausberg, near Misahoehe, Togo, December 7, 1904 (two sheets in Herb. Berl.); *Kling* 60, Jege, Bismarckburg, Togo, in 1889 (Herb. Berl.); *idem* 166, Jege, Bismarckburg, Togo, October 30, 1889 (Herb. Berl.).

Described by BUSSE as growing up to 2 m. in height, and by BUETTNER as reaching the height of a man, this species is seen to be one of the tallest

African species of *Coreopsis*. The type specimens have the exterior involucral bracts much larger than in BUSSE's specimens, being twice the length of the inner ones. The type has also larger leaves and ligulate florets, some of the ligules reaching 2 cm. in width, but all the other characters are too much alike to warrant specific and probably even varietal separation of the Busse plants. The achenial measurements are taken from BUSSE's plants, as the achenes of the type are immature.

Coreopsis bracteosa, sp. nov.—Herba glabra, verisimiliter perennis et 7–10 dm. alta, caulis internodiis folia superantibus, mediis inferioribusque saltem 18–22 cm. longis. Folia sessilia, indivisa, linearia, 6–20 cm. longa et 4–10 mm. lata, in apicem acutum sensim angustata, sparsim dentata dentibus saepe ad spinas vel etiam pilos spinulosos flexiles reductis, margine revoluta et interdum minutissime spinuloso-ciliata. Capitula pedunculata pedunculis maximam partem glabris, usque ad 5 cm. longis, radiata, pansa ad anthesin 3.5–4.5 cm. lata et 6–9 mm. alta. Involucri bracteae exteriores numerosae 19–21, anguste lineares, margine spinuloso-ciliatae, aliter glabrae, apice acerrime apiculatae, 1–1.7 cm. longae, interioribus lanceolatis dorso hispidis plerumque dimidio longiores. Flores ligulati circ. 12, ligula elliptici, lutei, apice denticulati, circ. 1.7–2 cm. longi et 5–7 mm. lati. Achaenia atra, linearia vel oblonga, valde compressa, plerumque alata, margine et supra ad faciem sursum hispida, corpore circ. 4–5 mm. longa et (alis inclusis) 1–1.5 mm. lata, biaristata aristis sursum hispidis 0.6–3 mm. longis. Planta C. abyssinicae Schz. Bip. affinis sed differt foliis indivisis non pinnatipartitis, involucri bracteis exterioribus 19–21 non tantum 12, etc.

Hans Meyer 532, bush and tree-grass-steppe, at altitude of 1200–1400 m., Jhangiro and Karagwe, German East Africa, summer of 1911 (type in Herb. Berl.).

A species closely allied to *C. abyssinica* Schz. Bip., but from the type collection (*Schimper* 332) and other specimens of that species in the Berlin Herbarium differing in its linear, undivided, not pinnately divided leaves, and in its large number (19–21) of exterior involucral bracts. Both species are alike in having some of the teeth on the leaves modified into structures intermediate between spines and hairs, several millimeters in length.

Coreopsis leptoglossa, sp. nov.—Herba annua, erecta, gracillima, speciminibus observatis parce ramosis, caule tetragono, glabro,

8–10 dm. alto. Folia petiolata, petiolis latis hispido-ciliatisque usque ad 7 mm. longis vel angustatis glabratisque usque ad 2.5 cm. longis, petiolo adjecto 5–9 cm. longa, glabra, bipinnata, segmentis linearibus, plerumque circ. 1 mm., rarius 1.5–2 mm. latis, apice acutis, margine non ciliatis sed parce revolutis. Capitula tenuiter pedunculata pedunculis 2–10 cm. longis, radiata, pansa ad anthesin 4–5 cm. lata et 6–9 mm. alta. Involucri bracteae basi dense aliter leviter hispidae setis acribus, arcuatis, multi (6–12)-loculatis, exteriores 8–10, lineares, apice acutae, margine maximam partem non ciliatae, 5–7 mm. longae et 0.6–0.9 mm. latae, interioribus lanceolatis plerumque breviores. Flores ligulati circ. 8, lutei, leptoglossati, ligula lineari-elliptici, apice integri vel obscure denticulati, 2–2.5 cm. longi et 4–6 mm. lati. Achaenia matura non observata; ovariis obovatis, valde compressis, late alatis, supra ad margines et medium erecto-hispidis, biaristatis; aristis erecto-hispidis, 0.4–0.7 mm. longis.

T. Kassner 2871, on mountain slope, Lofuku River, Congo Free State, May 25, 1908 (type in Herb. Berl.).

A species with the flowering heads resembling those of *Bidens Steppia*, especially as to involucre.

Cosmos microcephalus, sp. nov.—Herba annua, erecta, gracillima, plus minusve hispido-pubescens, caule simplici 2–3 dm. alto. Folia opposita petiolata petiolis 5–15 mm. longis, petiolo adjecto 1–3.5 cm. longa, bipinnata, segmentis linearibus vel linearilanceolatis, plerumque acutis. Capitula solitaria, longe tenuiterque pedunculata pedunculis 8–17 cm. longis (pro genere), parva, radiata, pansa ad anthesin 1.5–2.5 cm. lata et 8–12 mm. alta. Involucri bracteae in 2 seriebus dispositae; exteriores 6–8, lineares, obtuse calloso-apiculatae, glanduloso-hispidae, 4–6 mm. longae, interiores late lanceolatae, manifeste longiores. Flores ligulati circ. 5, flavi, late obovati, apice truncati vel emarginati, 8–12 mm. longi. Achaenia tenuissime linearia, atra vel versus apicem brunneo-straminea, superne in cervicem subcapilliformem sensim angustata, erecto-hispida, corpore (cervice adjecta) 1.6–2.2 cm. longo et inferne circ. 0.6 mm. lato, apice nunc biaristata aristis tenuibus retrorsum hamosis usque ad 2.3 mm. longis, nunc etiam calva.

Schiede 1561, cold regions, Mexico[10] (two type sheets, bearing about fifty small specimens, in Herb. Berl.).

Perhaps a depauperate form of a large plant. The technical characters, however, are singularly unlike those of any species described heretofore.

Coreopsis badia, sp. nov.—Herba glabra, ramosa ramis striatis. Folia ramorum sessilia, membranacea, 1.5–2.5 cm. longa, nunc cuneato-oblanceolata et versus apicem remote acriterque serrata, nunc irregulariter trilobata lobis lineari-oblongis. Capitula ramos singillatim terminantia, tenuiter pedunculata pedunculis 3–9 cm. longis, radiata, pansa ad anthesin ±2 cm. lata et ±7 mm. alta. Involucri glabri bracteae subaequales, exteriores 7–10, lineari-oblongae, acriter apiculatae, demum 5–7 mm. longae. Flores ligulati circ. 8, lutei, ligula lineari-elliptici, apice obscure denticulati, 7–10 mm. longi. Achaenia compressa, atra, corpore tenuiter vel sublate linearia, 5–9 mm. longa et 0.9–1.5 mm. lata, faciebus venuste adpresseque erecto-pilosa, marginibus (saltem achaenia exteriora) late et perspicue membranaceo-alata alis erecto-ciliatis, apice biaristata aristis tenuibus erecto-hispidis 3–4 mm. longis. Involucri bracteae interiores, paleae, achaeniorum alae badiae vel parce purpureo-badiae.

Mission of Gironcourt 256, on mountains of gneiss, Togo, 1908–1909 (type in Herb. Berl.).

The single specimen examined is a small flowering and fruiting branch coming from a more or less injured stem which, in turn, is seen to have grown from a prostrate rooting stem that previously had probably been trampled to the earth. The leaves studied, therefore, may not be strictly representative of those on normal specimens. The fruiting heads offer a strong general resemblance to those of the North American *Bidens coronata* (L.) Britt. (*Coreopsis trichosperma* Michx.).

Coreopsis cosmophylla, sp. nov. (pl. ix, figs. *h–n*).—Herba gracilis, glabra, verisimiliter 6–9 dm. alta, caule angulato, perspicue sulcato, apice parce ramoso, internodiis circ. 9–10 cm. longis. Folia subsessilia vel petiolata petiolo alato et usque ad 1.5 cm. longo, petiolo adjecto 4–8 cm. longa, pinnata; foliolis paucis (1 vel 2 jugis), linear-

[10] No other data were left by SCHIEDE, but the plants were collected between 1828 and 1836 (the dates respectively of his arrival in Mexico and of his death), and the locality lay without doubt within the triangular area reaching from Papantla and Orizaba at the east to Angangueo at the west (cf. HEMSLEY, Biol. Cent. Amer. **4**: 123. 1886).

ibus, versus basim maxime versus apicem minus attenuatis, apice acutis, breviter spinuloso-ciliatis, integerrimis vel lobo lineari-lobatis, lateralibus 1–2 mm. latis et usque ad 4.5 cm. longis, terminali 1.5–2.5 mm. lato et usque ad 6 cm. longo. Capitula pauca, radiata, pansa ad anthesin circ. 5 cm. lata et circ. 8 mm. alta, tenuiter pedunculata pedunculo 10–12 cm. longo. Involucrum glabratum, bracteis exterioribus circ. 8 vel 9, lineari-lanceolatis, supra inconspicue ciliatis, margine apiceque induratis, circ. 5–6 mm. longis; interioribus lanceolatis, circ. 7–8 mm. longis. Flores ligulati 8, lutei, ligula elliptici, apice minute 3-denticulati, 2–3 cm. longi. Achaenia non observata; ovariis oblongis vel orbiculato-ovatis, compressis, alatis, margine et apice sursum hispidis, biaristatis; aristis glabris vel ad medium sursum 1–2- spinulosis, 1.5–2 mm. longis.

Muenzner 159, Msamvia, Lake Tanganyika District, German East Africa, February 24, 1909 (type in Herb. Berl.).

GLOSSOGYNE TENUIFOLIA (La Bill.) Cass., Dict. Nat. Sc. **51**:475. 1827; *Bidens tenuifolia* La Billardiere Sertum Austr. Caled. 44. *pl.* 45. 1825; *B. Meyeniana* Walp., Nov. Act. Nat. Cur. 19. Suppl. I. 271. 1843.

The type of *Bidens Meyeniana*, collected by MEYEN at Cape Syngmoon, Kwangtung, China, August, 1831, is preserved in the Berlin Herbarium. WALPERS described it as being nearest to *B. parviflora* Willd., wherefore FORBES and HEMSLEY (Jour. Linn. Soc. **23**:435. 1888) stated that it might be referable to *B. parviflora* or to *B. bipinnata*. The plant, however, is typical *Glossogyne tenuifolia* Cass., and in fact the species has already been thus equated on a label for another specimen (legit HILLEBRAND) by some botanist (anonymous) in the Berlin Herbarium.

THELESPERMA MEGAPOTAMICA (Spreng.) O. Kuntze, Rev. Gen. Pl. **3**^{II}:182. 1898; *Bidens megapotamica* Sprengel Syst. Veg. **3**:454. 1826; *Thelesperma scabiosoides* Less. Linnaea **6**:512. 1831; *Bidens paradoxa* Don ex Hook. and Arn., HOOKER etc. Jour. Bot. **3**:319. 1841: *Bidens Leyboldii* Phil., Anal. Univ. Chil. **27**:338. 1865; non *Bidens megapotamica* O. E. Schulz, Engler Bot. Jahrb. **50**: Suppl. 182. 1914.

Recently O. E. SCHULZ (*loc. cit.*) found in the Herbarium of the Botanical Garden at Berlin three sheets of *Bidens* material collected by SELLO (the name often spelled "Sellow" in literature), no. 607, in Brazil. These he deter-

mined as *Bidens megapotamica* Spreng., although the labels bore no data as to the locality in Brazil whence the plants came. SPRENGEL's description, however, was based upon a plant collected by SELLO at "Rio Grande" in "Brazil."[11] That SCHULZ had not seen this Rio Grande specimen is shown by his citing it "Sellow ex Sprengel." HOOKER and ARNOTT (*loc. cit.*) definitely equated *Bidens megapotamica* Spreng. with *Thelesperma scabiosoides* Less., doubtless having seen an original SELLO specimen among the numerous SELLO specimens sent from Berlin to London and elsewhere. DECANDOLLE had earlier (Prodr. **5**:604. 1836) placed *Bidens megapotamica* under the heading "Species non satis notae," yet elsewhere (*loc. cit.* 634) he listed *Thelesperma scabiosoides* Less., which LESSING had founded upon a plant collected by SELLO in Brazil, "in provincia Rio Grande."

When we examine SPRENGEL's original description of *Bidens megapotamica*, it becomes evident that he did not have in mind the species of *Bidens* that SCHULZ later studied. SPRENGEL described the leaves (leaf divisions) as linear-filiform and the involucre as colored. The SELLO specimens studied by SCHULZ have the leaf segments linear to narrowly lanceolate, but in no case even slightly filiform. Their involucres are of the ordinary green or brown, and would never have called for SPRENGEL's adjective "colorato." Clearly, SPRENGEL had before him another plant collected by SELLO. Without question this other plant was the species named *Thelesperma scabiosoides* by LESSING, and based likewise upon SELLO's "Rio Grande" specimen.[12] Specimens of *T. scabiosoides*, or *T. megapotamica* as it must hereafter be called, have the leaf

[11] SPRENGEL Latinized the citation Rio Grande to read "Ad fl. magnum Amer. austr.," evidently thinking that a Rio Grande River had been meant by SELLO. The name *megapotamica* would seem to emphasize this fact. A study of various specimen labels, however, shows that SELLO collected many of his specimens either in the State of Rio Grande Do Sul or in the country just to the south, and which, although shortly after SELLO's collecting separated from Brazil under the name Uruguay, was considered as a part of Brazil when SELLO collected, and may easily have been considered by him as a part of the adjacent province of Rio Grande Do Sul. Thus we read (as given by LESSING, Linnaea **6**:103. 1831): "Sellow in Brasilia meridionali ad Rio Pardo Octbr. et Novbr. 1823"; *ibid.* 141, "In Monte Video Commerson et Sellow"; *ibid.* 516, "Sellow in Campis ad Rio Nigro." In this connection we may note also that DE CANDOLLE (Prodr. **5**:634. 1836) cites for the State of Rio Grande [Do Sul] four species of *Thelesperma* and *Isostigma* collected by SELLO and cited by LESSING merely as coming from Brazil.

[12] In the Berlin Herbarium are four SELLO sheets of *Thelesperma scabiosoides* Less. Two of them (nos. 874 and 1065), while originally labeled "Brasilia," have had "Montevidio" inserted in a later handwriting. Among the many other sheets are two of plants collected by Dr. OTTO KUNTZE at Villa Mercedes, Argentina, January 2, 1892, and labeled by him, "*Thelespermum megapotamicum* [*Th. scabiosodes-sic*-Less. 1831] O.K. (Spr. 1826)." The name *T. megapotamica* was published in 1898 by KUNTZE (*loc. cit.*), but was overlooked by the *Index Kewensis* and apparently by all other botanists until the present.

divisions linear-filiform and, in the dried state, the inner involucre is often purplish or blackish. In the Berlin Herbarium there are three sheets bearing PHILIPPI's original specimens of *Bidens Leyboldii* from Mendoza. These specimens all are clearly *T. megapotamica*.[13] The species of true *Bidens* erroneously referred by SCHULZ to *B. megapotamica* Spreng. is found referable to *B. subalternans* DC. as given in SCHULZ's own treatment (*loc. cit.* 181). From these and various other specimens, a partial list of which is given below, the following amplified description is drawn:

BIDENS SUBALTERNANS DC., descrip. amplif.—Herba annua, erecta, ramosa, 7–10 (verisimiliter usque ad 20) dm. alta, caule tetragono glabro vel sparsim hispido. Folia petiolata, petiolis usque ad 3.5 mm. longis, petiolo adjecto 6–18 cm. longa, bipinnatifida, segmentis membranaceis, breviter et dense vel remote hispidis, plus minusve dentatis vel irregulariter lobulatis, infra pallidioribus, terminalibus plerumque elongato-lanceolatis vel elongato-linearibus, acuminatis, lateralibus saepe angustioribus. Capitula non numerosa, ramos terminantia, pedunculata pedunculis 1–4 cm. longis, discoidea vel subradiata, ad anthesin 8–10 mm. lata et 5–6 mm. alta, demum cum achaeniis circ. 1.7 cm. lata et circ. 1.6 cm. alta. Involucri bracteae subaequales, exteriores circ. 8, lineares, ciliatae, plus minusve hispidae, acute vel subobtuse calloso-apiculatae, demum 4–6 mm. longae, interiores lineari-lanceolatae. Flores ligulati albidi et rudimentarii vel saepe absentes. Achaenia non pauca (30–50) in capitulo, linearia, tetragona, sulcata, atra, glabra vel superne leviter hispida, corpore exteriora 6–8 interiora 8–14 mm. longa et paleas facile superantia, 2–4 aristata aristis suberectis retrorsum hamosis 1–2.5 mm. longis.

Sello 607, Brazil (three sheets in Herb. Berl.); *Gardner* 3851, Prov. Goyaz, Brazil, 1841 (Herb. Berl., Bois.); *Bettfreund* and *Köster* 460, Almagro-Flores, Buenos Aires (Herb. Berl.); *G. Hieronymus*, Sierra chica de Córdoba, Colanchanga, Prov. Córdoba, Argentina, February, 1882 (Herb. Berl.); *F. Schickendantz* 57,[14] Yacatula, Prov. Catamarca, Argentina, March, 1879 (Herb.

[13] It is a pleasure to acknowledge the courteous assistance of Miss ETHELYN M. TUCKER, librarian of the Arnold Arboretum, who has forwarded to me a copy of the original description of *Bidens Leyboldii*.

[14] *Idem* 16, included here by O. E. SCHULZ, differs in its slender fruiting heads with their few (5–15) achenes and is referable to *B. exigua* Sherff, a South American species close to the North American *B. leptocephala* Sherff, but having among other distinctions the external involucral bracts much less diminutive.

Berl.); *Otto Kuntze*, Dique, Córdoba, Argentina, December, 1891, capitulis monstrosis (Herb. Berl.); *C. Galander*, Córdoba, Argentina, March 15, 1878 (Herb. Berl.); Schnyder 922, Buenos Aires, Argentina (Herb. Berl.); Herb. JOHN MIERS, Buenos Aires and Mendoza, Argentina (Herb. Brit. Mus.).

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EXPLANATION OF PLATES VI–IX

PLATE VI

Isostigma glycinaefolium: a, fruiting specimen, ×0.66; *b*, slightly dentate leaf, ×0.66; *c*, exterior involucral bract, ×4; *d*, interior involucral bract, ×4; *e*, palea, ×4; *f*, mature achene, ×4; *a*, from Riedel's specimen in Herb. Schz. Bip. in Herb. Mus. Hist. Nat. Paris; *b-f*, from Riedel's specimen (BAKER's type), in Herb. Kew.

PLATE VII

Coreopsis oblonga: a, main portion of flowering specimen, ×0.8; *b*, lower leaf from *a*, ×0.8; *c*, exterior involucral bract, ×4.8; *d*, interior involucral bract, ×4.8; *e*, ligulate floret and portion of ovary attached, ×2.4; *f*, palea, ×4.8; *d*, disc floret with immature achene, ×4.8; all from Alex. Carson 106, type, in Herb. Kew.

PLATE VIII

Heterospermum rhombifolium: a, specimen with flowers and fruits, ×0.76; *b*, exterior involucral bract, ×3; *c*, interior involucral bract, ×3; *d*, palea, ×3; *e*, disc floret, ×7.5; *f*, outermost, *g*, intermediate, and *h*, innermost achenes, ×3; all from W. Lechler 1576, in Herb. Mus. Hist. Nat. Paris.

PLATE IX

Bidens leptolepis: a, flowering specimen, ×0.67; *b*, exterior involucral bract, ×2.7; *c*, interior involucral bract, ×2.7; *d*, ligulate floret, ×2.7; *e*, palea, ×2.7; *f*, disc floret, ×2.7; *g*, ovary, ×8; all from Kassner 2725, type, in Herb. Berl.

Coreopsis cosmophylla: h, flowering specimen, ×0.67; *i*, exterior involucral bract, ×2.7; *j*, interior involucral bract, ×2.7; *k*, ligulate floret, ×2.7; *l*, palea, ×2.7; *m*, disc floret, ×2.7; *n*, ovary, ×6.7; all from Muenzner 159, type, in Herb. Berl.

SHERFF on COMPOSITAE

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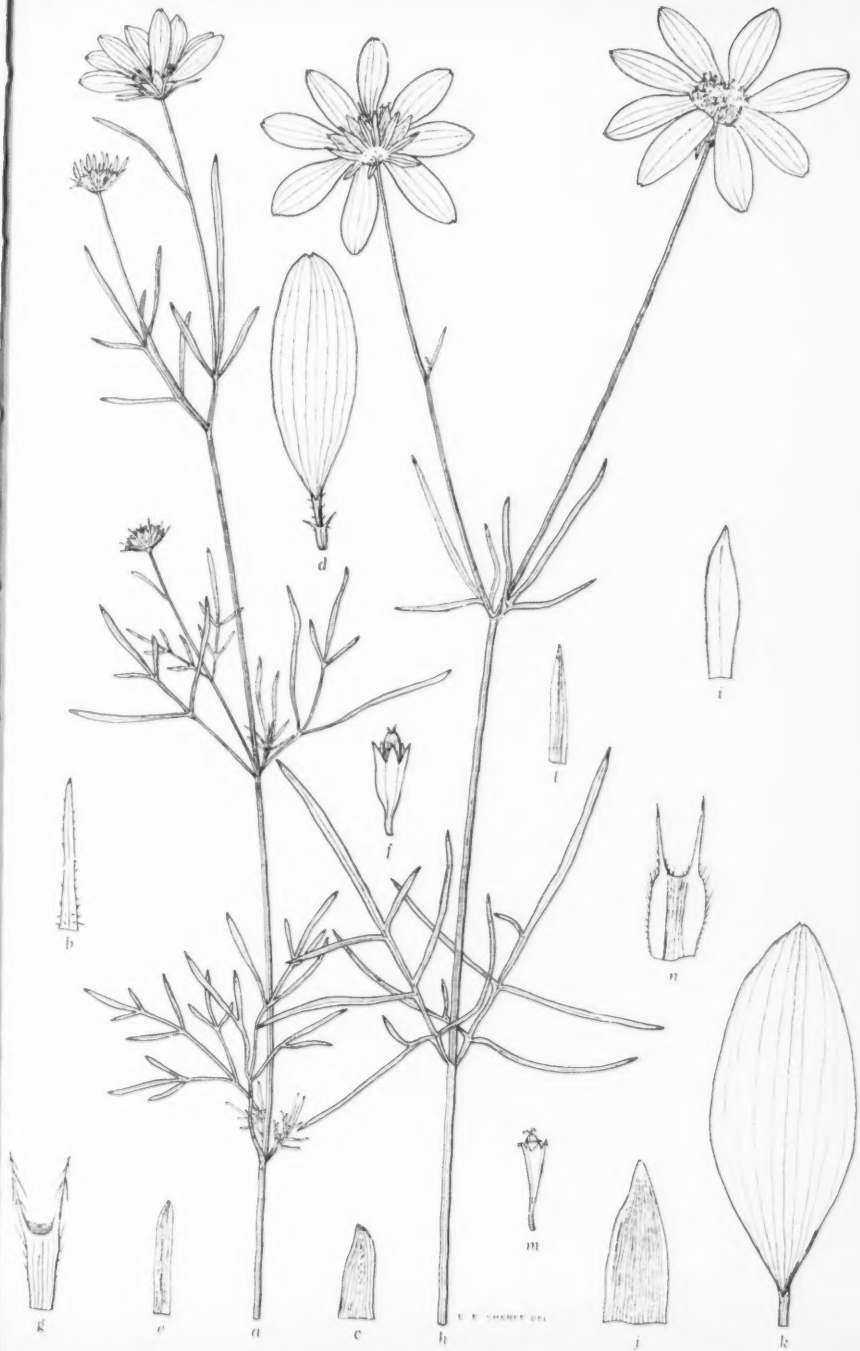

SHERFF on COMPOSITAE

IS GASEOUS NITROGEN A PRODUCT OF SEEDLING METABOLISM[1]?

JEHIEL DAVIDSON

Growth is the difference between assimilation and dissimilation. The sources of dissimilation common to plants and animals are the fats and carbohydrates. In animal life the proteins are an important source of dissimilation, the waste nitrogen products being eliminated mainly as urea, uric acid, and hippuric acid. With reference to plants, the question whether the proteins participate in respiration, which is the principal form of dissimilation in plant life, is somewhat unsettled. The chief difficulty in settling this question lies in the fact that the plant proteins, even if they do serve as respiratory material, are not eliminated, at least in their main bulk, as waste products, but the products of decomposition are re-assimilated, with the formation of new proteins. The actual loss of nitrogen, if any, would therefore be small.

The question as to possible small losses of nitrogen in a gaseous form from plants also remains unsettled, however, owing principally to lack of adequate methods of attack. The direct measurement of small quantities of gaseous nitrogen, should such be formed in the process of respiration, would prove to be extremely difficult, in view of the large volume of atmospheric nitrogen which would have to be passed through the controlled system in which the plants were growing. A synthetic atmosphere with a greatly reduced proportion of this element would create abnormal conditions, and would also be likely to injure the plants.

Losses of nitrogen from growing plants have been found by a number of investigators. WILFARTH, RÖMER, and WIMMER (7) have established such losses for barley, spring wheat, peas, and mustard. The nature of this loss has not been determined, but these investigators are inclined to think that the lost nitrogen migrates back to the soil. They base their view on the fact that potassium and sodium, which are not known to form any volatile

[1] Presented at the fall meeting of the American Chemical Society, Pittsburgh, September 1922.

compounds, are lost simultaneously with nitrogen. LIEBSCHER (5) believes that this loss of nitrogen is physical or mechanical in nature, due largely to the dying and falling off of certain parts of the plants as they approach maturity. Neither of these hypotheses, however, excludes the possibility of the escape of nitrogen in a gaseous form during the metabolic processes which are taking place in the plant, as the loss of this element may not necessarily be limited exclusively to one source. Several investigators have attempted to solve the question whether nitrogen in some gaseous form is lost from plants during germination and early growth of the seedling. The results reported are contradictory. BOUSSINGAULT (2), LAWES, GILBERT, and PUGH (4), and HELLRIEGEL (3) found no loss of nitrogen, while SCHULZ (6) and ATWATER and ROCKWOOD (1) reported such a loss under presumably the same conditions. Moreover, these investigators are not concerned with the question of whether this loss is inherently physiological in character, or is due to microbiological activity and other environmental factors.

It was the object of this work to determine whether or not nitrogen is lost to the air as an inherent function of the metabolic processes during the early life of the plant, beginning with germination. This period of growth was chosen because it is considered the most critical, from the standpoint of intensive breaking up of nitrogenous substances present in the seeds, and their transformations and translocation in germination and in the early days of the seedling. Also, this period allows an expedient method of attacking the problem, and makes it possible to work out the principles involved with the least interference from modifying factors.

WHEAT SEEDLINGS GROWN UNDER NON-STERILE CONDITIONS.—The seed used was a "Fultz" soft winter wheat grown in Arlington. In order to avoid any possible loss from transference during analysis, the seedlings were grown directly in Kjeldahls. The tall flasks also served as a perfect protection from any mechanical loss. The seed was weighed in quantities as close as possible to 2 gm., and placed in the Kjeldahls, which contained enough distilled water for germination, more being added from time to time in quantities sufficient to sustain normal growth. At certain intervals the contents of a number of Kjeldahls, consisting of growing seedlings mixed with ungerminated seed, were analyzed for nitrogen

without any disturbance of the analytical material. Ten nitrogen analyses of the original seed were made at the same time. The results are given in table I.

TABLE I

PERCENTAGE OF NITROGEN IN GROWING SEEDLINGS AS COMPARED WITH UNGERMINATED SEED

No.	Nitrogen in growing seedlings		Nitrogen in ungerminated seed
	No. of seedlings	Percentage of nitrogen	
	3 days		
1	21	1.86	1.87
2	36	1.78	1.84
3	30	1.94	1.88
4	15	1.81	1.94
5	28	1.89	1.86
		Average 1.86	1.88
	6 days		
6	25	1.82	1.93
7	25	1.94	1.80
8	17	1.80	1.87
9	24	1.83	1.86
10	16	1.84	Average 1.87
		Average 1.84	
	11 days		
11	29	1.90	
12	19	1.97	
13	18	1.86	
14	18	1.82	
		Average 1.89	

The number of seeds that developed seedlings varied in the fourteen experimental Kjeldahls. No correlation is shown between the number of seedlings and the individual nitrogen fluctuations, nor between the age of the seedlings and the nitrogen fluctuation. The three-days old seedlings appear to give a slightly higher nitrogen average than the six-days old seedlings, but the eleven-days old seedlings seem to give the highest average. The differences are slight, however, and well within the limits of experimental error. Moreover, the average of all the fourteen Kjeldahls in which the seedlings were grown, as well as the limits of individual fluctua-

tions, is practically identical with the average and limits of fluctuation of the ten nitrogen determinations on the original seed.

WHEAT SEEDLINGS GROWN UNDER STERILE CONDITIONS.—The environmental conditions in the Kjeldahls seemed to be very favorable for fungous growth, and the ungerminated seed and the bases of the seedlings were overgrown with different kinds of fungi, especially those of the *Aspergillus* type, which are believed by some investigators to be capable, under certain conditions, of fixing atmospheric nitrogen. Consequently there was the remote possibility that the loss of nitrogen in gaseous form might be exactly compensated by a gain through fixation of atmospheric nitrogen. It was felt, therefore, that the experiment just described should be repeated under sterile conditions.

METHOD OF STERILIZING SEED.—Several attempts to grow seedlings under sterile conditions failed. The weighed seed was sterilized in test-tubes with a mercuric chloride solution, washed with sterile water, and transferred into sterilized Kjeldahls. On the fourth or fifth day contamination manifested itself through fungous growth. The contamination probably took place during the relatively long exposure to which the sterilized seed was subjected in this procedure. Finally, the following method was devised and found to give satisfactory results. Pieces of glass tubing about three inches long and three-quarters inch in internal diameter were fitted at one end with disks made of Whatman filter paper. The disks were fastened to the tubes by two crossing rubber bands running from end to end. The tubes containing the weighed seed were immersed in a 1:1000 solution of mercuric chloride, which filtered in from the lower end through the filter paper. After remaining in the sterilizing solution for twenty minutes the tubes were lifted up, allowing the solution to run out through the filter paper, and then immersed consecutively in two flasks containing sterile distilled water. The tubes with the sterilized and washed seed were then inserted in the neck of sterilized Kjeldahls containing a little distilled water, which had previously been saturated with calcium carbonate to overcome its inherent toxicity. The rubber bands were then snapped off and the paper disks and the seed fell to the bottom of the Kjeldahls, which were quickly plugged with the cotton plugs originally provided.

A "Purple Straw" soft winter wheat, grown in Arlington, was used in this experiment, and the quantities were close to 1 gm. Of the ten Kjeldahls originally started, two were lost and two showed a slight fungous contamination toward the end of the experiment. The seedlings were allowed to grow for fifteen days and were analyzed for nitrogen as before. Ten nitrogen determinations were made on the original seed, sterilized exactly as before but analyzed immediately, as well as ten on untreated original seed. The results are given in table II.

TABLE II

PERCENTAGE OF NITROGEN IN WHEAT SEEDLINGS GROWN UNDER STERILE CONDITIONS AS COMPARED WITH STERILIZED AND UNTREATED SEED

No.	NITROGEN IN GROWING SEEDLINGS		PERCENTAGE NITROGEN IN STERILIZED SEED	PERCENTAGE NITROGEN IN UNTREATED SEED
	No. of seedlings	Percentage nitrogen		
1	22	2.07	2.03	2.00
2	22*	2.02	1.93	1.97
3	26*	2.07	1.97	1.97
4	21	2.02	2.10	1.93
5	15	1.95	2.03	1.99
6	11	1.96	2.04	1.93
7	14	2.04	2.08	1.97
8	15	2.05	1.94	2.05
9			2.06	1.92
10			2.01	2.04
		Average 2.02	2.02	1.98

* Slightly contaminated.

The nitrogen content of the growing seedlings and that of the sterilized seed are identical. The nitrogen content of the untreated seed is slightly lower than that of the others, but the difference is well within the limits of experimental error. The limits of individual fluctuations of nitrogen content are practically the same in all three sets of determinations. It is of interest to note that no nitrogen was lost in the process of sterilization. The results obtained in this experiment are in full accord with those obtained previously. No loss of nitrogen could be observed in either case.

COW PEA SEEDLINGS GROWN UNDER STERILE AND NON-STERILE CONDITIONS.—The experiment was repeated with cow pea seedlings, for the reason that this plant belongs to another class, and its seed

is larger and relatively richer in nitrogen than wheat seed. The experiment is especially significant in view of the fact that ATWATER and ROCKWOOD (1) reported appreciable losses of nitrogen from peas during germination and early growth of the seedlings. The procedure was exactly the same as in the previous experiments, with the exception that the pulp of two Whatman 9 cm. filter papers was placed in each Kjeldahl to serve as a seed bed. Twelve weighed cow pea seeds were used in each case. The seedlings were allowed to grow for about fifteen days. Of the ten replicates

TABLE III

PERCENTAGE OF NITROGEN IN COW PEA SEEDLINGS GROWN UNDER STERILE AND NON-STERILE CONDITIONS AS COMPARED WITH STERILIZED AND UNTREATED SEED

No.	NITROGEN IN SEED		NITROGEN IN SEEDLINGS			
			UNDER STERILE CONDITIONS		UNDER NON-STERILE CONDITIONS	
	Percentage in sterilized seed	Percentage in untreated seed	No. of seedlings	Percentage nitrogen	No. of seedlings	Percentage nitrogen
1.....	3.83	3.93	4	3.86*	3	3.91
2.....	4.11	3.88	3	3.84*	4	3.90
3.....	3.89	3.98	.....	Lost	6	3.81
4.....	4.02	3.91	.....	Lost	3	3.81
5.....	3.91	3.84	4	3.95	5	3.95
6.....	3.70	3.93	.....	Lost	4	3.87
7.....	3.65	3.84	12	4.02	7	3.77
8.....	3.88	3.86	9	3.85	6	3.77
9.....	3.85	3.87	6	3.91*	8	4.06
10.....	3.84	3.77	.....	Lost	4	4.00
	Average 3.87	Average 3.88		Average 3.90		Average 3.88

* Contaminated.

which the investigator attempted to grow sterilly, six showed contamination with *Fusarium*, *Rhizopus*, and *Penicillium* types toward the close of the experiment. On the whole, however, the seedlings grown under sterile conditions were more vigorous and healthy than those grown under ordinary conditions. The number of seeds that developed seedlings varied, but on the whole germination was better under sterile conditions than under non-sterile conditions. The results are given in table III.

Unfortunately, four nitrogen determinations in the sterile seedling series were lost. Of the six Kjeldahls left, three showed

no contamination. The general average, as well as the limits of individual fluctuations of the nitrogen content, is practically identical in all four sets of determinations. Furthermore, the individual fluctuations are entirely independent of the number of the seedlings, as well as of the degree of contamination in the sterile seedling series. As with the wheat seedlings, no loss of nitrogen from growing cow pea seedlings could be observed.

One would be justified, therefore, to draw the conclusion that no nitrogen in gaseous form is lost during the early life of the seedling when it is left to depend entirely on the food materials stored in the mother seed. While the results of these experiments might be modified by various normal or abnormal factors in plant growth, the loss of nitrogen in gaseous form would not seem to be an inherent characteristic of the metabolic processes in the young seedling.

Summary

Wheat seedlings and cow pea seedlings were grown in Kjeldahl flasks under sterile and non-sterile conditions. The results indicate that no nitrogen in gaseous form is lost in the process of germination and in the early life of the seedlings as an inherent function of their metabolic processes.

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Washington, D.C.

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EXTRA-FLORAL NECTAR GLANDS OF RICINUS COMMUNIS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 310

E. L. REED

(WITH TWELVE FIGURES)

On the castor-oil plant there are two distinct types of extra-floral nectar glands. One type is large, stalked, and distinctly visible to the naked eye, found on the petioles, the stems at the base of the petioles, and the blossom spike. The other type is scarcely discernible without the aid of a hand lens, sessile, found sparingly on the lower side of the leaf blade about 1 cm. from the margin (but with no regularity), and on the tips of each tooth of the margin.

After discussing the nature and abundance of the glandular hairs in the Euphorbiaceae, SOLEREDER states as follows:

> Glandular organs of a different type are much commoner among the Euphorbiaceae than the glandular hairs described above, namely, rather large external glands (nectaries), which are visible to the naked eye. . . . . Firstly they occur at the base of the petiole, where two or more of them are situated. Not uncommonly, however, they replace the stipules, or in certain species they surmount them. . . . . In other cases they are found at the base of the lamina, sometimes occurring on special lobes of the latter. Occasionally they are shifted higher up on the lamina, two or more of them being present on the lower side of the leaf; they are rarely met with on the upper side, but frequently occur on the leaf teeth.
>
> The anatomical structure of these glands has hitherto been little investigated; the chief work is that of FROMBLING on the Crotoneae. This author classifies the glands as patelliform and morulose . . . . the glands may be either stalked or sessile. . . . . The secretions of these glands are often considerable and lasting; in some cases, however, the glands are only functional during the early stages of the organs on which they occur.

The glands discussed in the present paper are both patelliform and morulose. The morulose appear on the cotyledons, but the patelliform only on the later leaves. No morulose glands appear on the stem at the base of the cotyledons.

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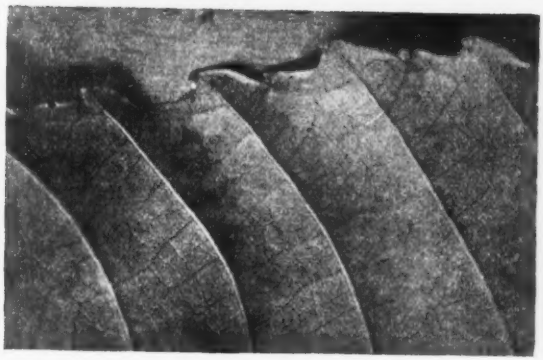

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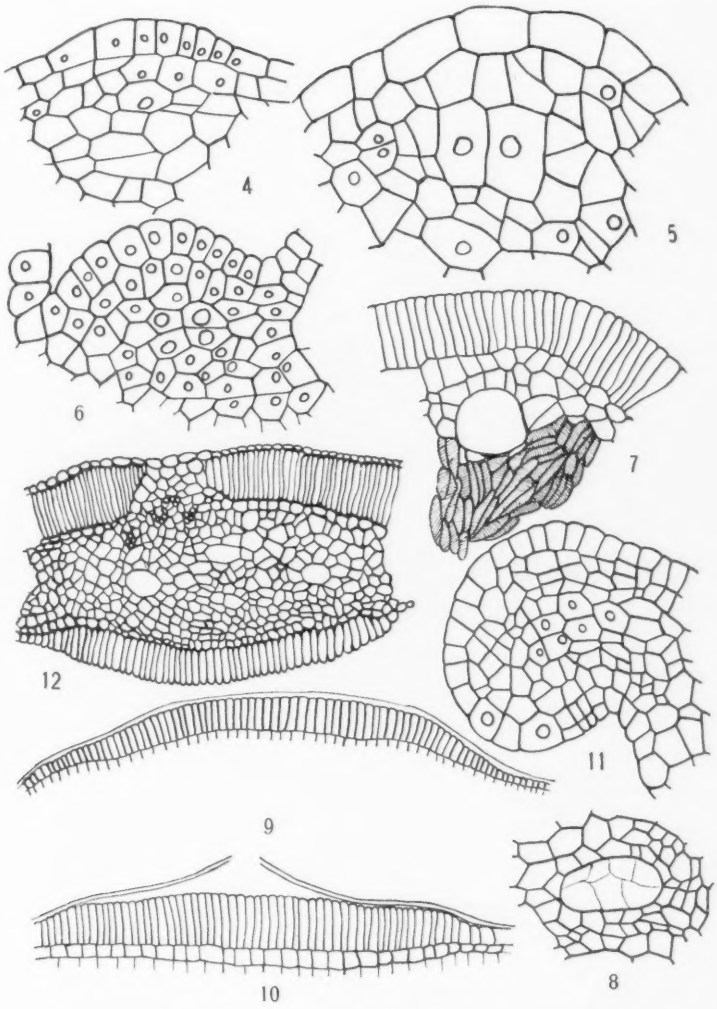
FIGS. 1–3.—Morulose and patelliform glands

In discussing *Ricinus sanguineus*, REINKE says: "From the appendages formed on the petiole little drops of a nectar-like fluid stand out; on the teeth of the leaf blade I can discern secretions of no sort on the developed leaf."

Clear crystal drops can plainly be seen on the morulose glands, and small drops easily discernible with a small hand lens can be seen on the patelliform glands of the leaf teeth and blade of *Ricinus communis* when the leaves are four or more weeks old. A small red ant is the only insect commonly seen visiting these glands. Fig. 1 shows the morulose glands about natural size on the petiole and at its base on the stem, and fig. 2 shows them slightly enlarged on the blossom spike, while fig. 3 shows the patelliform glands, enlarged, on the tips of the teeth. The morulose glands are well along in their development before the leaves have freed themselves from the enveloping bract; hence it was necessary to collect the youngest buds and section them in toto to discover the initial stages of the glands. They are of cortical origin, and when mature are well supplied with vascular bundles. Their organogeny is as follows.

One or more cortical cells in the second or third row below the epidermis is differentiated from the others by an increase in size and density of protoplasm (figs. 4, 6). These cells divide and the long axes of the resulting cells are at right angles to the epidermis (fig. 5). As soon as the initial cells are differentiated, the epidermal cells immediately above become larger and are distinguished from the neighboring cells (fig. 4). This enlargement of the initial cells and of those of the epidermis causes a distinct swelling of this portion of the surface. As the growth continues the glands become more and more raised above the surface, until they form distinct outgrowths varying in size from about 1 mm. in diameter on the blossom stalk to 3 mm. or more on the petiole and stem. The growth continues in such a manner as to form a knoblike structure. Vascular strands branch from the main bundles of the petiole or stem, and pass out into the glands, after which they branch profusely and extend to all parts, ending near or in contact with large storage cells which lie about two or three cells deep below the surface (fig. 7). These storage cells are formed by the



FIGS. 4–12.—Figs. 4, 5, 6, and 11, early stages in development of glands; fig. 7, termination of vascular bundles near storage cells; fig. 9, epidermis of gland, showing normal and palisade-like cells; fig. 10, rupturing of cuticle due to secretion of nectar; fig. 12, section through gland of under side of leaf blade.

absorption of the walls of two or more adjacent cells (fig. 8). The epidermal cells that form the secreting region are differentiated like a palisade, and occupy the central part of the surface of the gland; the remaining epidermal cells are normal (fig. 9). A thick cuticle covers these cells at the beginning of the active stage, and the secretion raises the cuticle blister-like, finally rupturing it, and appearing on the surface as a clear shining crystal-like drop of nectar (fig. 10).

The patelliform glands are found on the under side of the leaf blade in small numbers, and on all teeth of the margin. In the early development of a leaf the vascular bundles reach the margin with no sign of gland structure, but as the leaf enlarges initial cells appear (fig. 11), and the glands follow the same general mode of development as described for the morulose. The patelliform glands of the under side of the leaf are situated directly over a veinlet (fig. 12).

SUMMARY.—(1) The glands appear on all leaves, petioles, and stems; (2) they are all functional, at least in early stages; (3) they are constantly visited by a small red ant in search of nectar.

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CURRENT LITERATURE

NOTES FOR STUDENTS

Forests of the Himalayas.—The slopes of the mountains of northern India have the unique distinction of affording a mesophytic transition between torrid plains with an alternation of hot dry months and heavy periodic monsoon rains, and the high arid steppes of the Tibetan plateau. In such a transition region in the Garhwal district, OSMASTON[1] has made what is one of the first attempts to classify a portion of the forests of the Himalayas on a purely ecological basis. The region under consideration ranges from 2,500 to 15,000 feet in altitude, and includes over 2,500 square miles of forested lands, distributed over four zones, distinguished as (1) Tibetan with less than 10 inches of annual precipitation, (2) arid with 10–15 inches, (3) dry with 15–40 inches, and (4) moist with 50–80 inches. Five forest formation types are distinguished, described, and divided into associations, as follows: (1) The *Caragana-Lonicera-Artemisia* formation, which lies within the Tibetan zone at 9,000–15,000 feet, and is characterized by shrubs with flexible procumbent branches, deciduous foliage, and the absence of trees and grasses. (2) The *Betula-Rhododendron* formation, which is found mostly in the dry and arid zones at 9,000–13,500 feet, with a more humid atmosphere than the preceding, and characterized by rather dense stands of small trees and shrubs with deciduous foliage having various adaptations to retard transpiration. The best and most mesophytic association is the *Betula-Abies*, in which an open upper story of *Abies Webbiana*, with a height of 60–100 feet, has below it a lower stratum of *Betula utilis*, 30–50 feet high, and an undergrowth of shrubby *Rhododendron campanulatum*, and *Pyrus foliosa*. (3) The *Pinus-Cedrus* formation, which is developed in the dry and arid zones (6,500–12,000 feet), being forests somewhat xerophytic in appearance of rather open stands of such coniferous species as *Cedrus deodara*, *Pinus excelsa*, *Cupressus torulosa*, and *Picea Morinda*, together with deciduous dicotyledonous trees that sometimes form a lower story. The undergrowth varies from grasses in the more arid areas to shrubs in the more moist situations. (4) The *Quercus-Abies* formation occurring in the moist zone (5,000–11,500 feet), a mesophytic forest of good height, with *Abies Pindrow*, one of the chief species, ranging 140–200 feet in height. The dominants are conifers and evergreen oaks, but with secondary species largely deciduous, and epiphytic ferns and mosses in abundance. (5) The *Shorea-Anogeissus-Pinus* formation, in the moist zone, distributed in valleys up to 6,500 feet, with a subtropical climate

[1] OSMASTON, A. E., Notes on the forest communities of the Garhwal Himalaya. Jour. Ecology **10**:129–167. *pls. 3–16*. 1922.

and a rather xerophytic aspect. It is a rather open forest of conifers or trees more or less leafless during the hot weather preceding the monsoon rains, the undergrowth being largely of grasses. High temperature and the frequent occurrence of forest fires are factors of importance in this formation, and tend to increase its xerophytism. *Pinus longifolia* is the chief tree, often in pure stands, attaining a height of 70–140 feet, and possessing thick bark, excellent coppicing powers, and rapid growth while young, characters that enable it to withstand fires. This last formation has been made the subject of more detailed examination by KENOYER.

In an adjacent region KENOYER[2] has investigated an area with forests similar to those of the last two formations of OSMASTON. He distinguishes three forest types or formations developing in the region between 4,000 and 5,000 feet in altitude, and outlines the xerarch and hydrarch successions leading to a climax *Quercus incana* forest, corresponding to the *Quercus-Abies* formation of OSMASTON, which reaches its lowest altitudinal limits in the Sat Tal valley, and to a climax monsoon forest of *Bauhinia* and *Shorea* here at its upper limits. The *Pinus longifolia* forest is regarded as a pre-climax stage developing under conditions of poor soil, low humidity, and high insolation. That the Sat Tal valley represents a tension line between the plains and the montane region is shown by the development within its limits of the montane *Quercus incana* forest, characterized by KENOYER as a broad sclerophyllous type suited to places of no very great extremes of moisture or temperature, and also of the monsoon type, almost leafless at the beginning of the rains and adapted to great extremes of humidity. The rainfall responsible for this vegetation shows a yearly average of 85 inches, with 15 per cent or less coming within the eight dry months, October to May inclusive.

In addition to the broader generalizations relating the various forest formations to each other, OSMASTON gives many interesting details regarding the different associations and principal species, while KENOYER presents observations regarding periodicity within the monsoon forest. He distinguishes three distinct seasonal groups of herbaceous vegetation: (1) the spring, appearing with the rise of temperature and composed mainly of representatives of such temperate zone families as Ranunculaceae, Cruciferae, Violaceae, Geraniaceae, and Rosaceae; (2) the summer, coming with the monsoon rains, consisting mainly of representatives of tropical families such as Begoniaceae, Gesneriaceae, Orchidaceae, and Scitaminaceae; and (3) the autumnal, in the cooler weeks following the monsoon, in which representatives of the temperate zone appear from such families as the Compositae and Labiatae. He also calls attention to the fact that in the monsoon forest, practically leafless at the coming of the rains, in at least twenty of the forest species, including *Bauhinia* spp., *Erythrina suberosa*, *Ougeinia dalbergioides*, and *Stercufunalia* spp., the leaf

[2] KENOYER, L. A., Forest formations and successions in the Sat Tal valley, Kumaon, Himalayas. Jour. Ind. Bot. 2:236–258. *figs. 21.* 1921.

buds do not open until the fruit is mature. This forest abounds in lianas, epiphytes, strangling figs, and parasitic seed plants. Both contributions are to be commended for the well organized form in which the interesting data are presented.—GEO. D. FULLER.

Myrmecophytes.—Many scientists have been of the opinion that the whole subject of the mutual adaptations and relations of plants and ants is in need of thorough revision, and resultant investigations of the true ecological meaning and probable origin of some of the cases of apparent or true symbiosis of certain plants and certain species of ants have led to the appearance of a series of interesting articles. That by BEQUAERT[3] is of fundamental importance, since it is an attempt to summarize what is known at present of the relations that exist between ants and vegetation, and the extent of the research involved is indicated by a bibliography of nearly 1200 citations.

Limiting the term "myrmecophyte" to those plants that provide "myrmecodomatia," or special shelters for their ant guests, the author finds in Africa, the special field of his investigations, 42 such plants, represented by 7 families and 12 genera. Among these the Rubiaceae have 26 species, 15 belonging to *Cuviera*.

The myrmecodomatia consist either of (1) swollen stipules forming a pouch, (2) leaves providing pouches, (3) hollow stems externally normal, or (4) hollow stems with various swellings. The BELT-DELPINO hypothesis, as modified and supported by SCHIMPER, regards these domatia and the possession of glandular "food bodies" by myrmecophytes as adaptations for enlisting the services of an aggressive army of ants which protect the sheltering host plants against the attacks of leaf-cutting ants and other enemies.

BAILEY[4] has examined this and other hypotheses which attempt to explain myrmecophytism as a symbiosis, and fails to find any causal relation between the production of various ant shelters, extra floral nectaries, or food bodies, and the presence of the ants. He also fails to find evidence of the careful or efficient defence of the host plants by the sheltered ants, although conflicts with intruders doubtless occur. He concludes that the relationship is purely a case of parasitism, in which all the advantages lie with the ants. This conclusion is also supported by evidence obtained from a study of certain South American myrmecophytes reported through this journal.[5] That the glandular food bodies or "Müllerian corpuscles" produced on the base of the petiole and

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[3] BEQUAERT, J., Ants in their diverse relations to the plant world. Bull. Amer. Museum Nat Hist. **45**:333–583. *pls. 26–28. figs. 77–100.* 1922.

[4] BAILEY, I. W., The anatomy of certain plants of the Belgian Congo with special reference to myrmecophytism. Bull. Amer. Mus. Nat. Hist. **45**:585–621. *pls. 30–45.* 1922.

[5] ———, Notes on neotropical ant-plants. I. *Cecropia angulata*, sp. nov BOT. GAZ. **74**:369–391. *figs. 8.* 1922.

used for food by the ants are not allurements for these creatures acquired by natural selection is indicated by the fact that they are found on plants not frequented by ants. In the former of these articles BAILEY states that, although fungi are present in the domatia of the African myrmecophytes and are cut back by the ants, there is no evidence that this is other than the usual operation of cleaning their abodes. These abodes are also characterized by the presence of certain pads of wound tissue or callus-heteroplasias formed by the removal of medulla and xylem by the ants. The cell contents of such tissue may furnish some food for the ants.

In an earlier article BAILEY[6] has shown that the true fungus-growing and fungus-feeding habits ascribed to these creatures must be limited to certain highly specialized leaf-cutting Attine ants first described by BELT.

WHEELER[7] has also examined the evidence that ants plant, tend, and inhabit gardens of epiphytes, and that certain epiphytes are found only in such gardens. He found that ants of various kinds nest among the roots and leaves of such plants, and by transporting soil particles to the vicinity of these nests promote the growth of the epiphytes. He also found that no plants were present in the "ant gardens" that did not occur elsewhere, and that no ant species were limited to garden abodes. The colonizing habits of the ants, especially the founding of the colony by a single fertilized queen, made the planting of one garden from another a practicable impossibility. Consequently, in the absence of any actual observations of the origin of such epiphytic gardens, he concludes that the association of ants and epiphytes is accidental and sporadic.—GEO. D. FULLER.

Plant sociology.—The segregation of one phase of ecology and the attempt to regard this as a separate branch of biological science is perhaps but the erection of a milestone along the highway of progress. Although this distinction has not very generally been recognized in America, PAVILLARD[8] in a recent historical sketch has dated the rise of plant sociology, or phytosociology, from a paper of HARPER'S[9] in 1917. Since that time it has been developed principally by such members of the Zurich-Montpellier school as RUBEL, BRAUN-BLANQUET, LUDI, and PAVILLARD, in their attempt to focus attention upon the vegetation itself, to the exclusion of the habitat factors. Some of the earlier contributions have been noted previously in this journal.[10]

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[6] BAILEY, I. W., Some relations of ants and fungi. Ecology **1**:174–189. 1920.

[7] WHEELER, W. M., A new case of parabiosis and the "ant gardens" of British Guiana. Ecology **2**:89–103. *figs.3*. 1921.

[8] PAVILLARD, J., Cinq ans de phytosociology. Montpellier. pp. 30. March 1922.

[9] HARPER, R. M., The new science of plant sociology. Sci. Monthly **4**:456–460. 1917.

[10] BOT. GAZ. **70**:183–185. 1920; **71**:403–405. 1921.

In the present sketch the author repeats his emphasis[11] upon the association as a fundamental unit of phytosociology, welcomes TANSLEY's suggestion that this unit be regarded as a "quasi-organism," pays a tribute to the influence of the Anglo-American school in stressing the dynamic principle of interpretation, and approves of the introduction of a definite treatment of succession by LUDI and by ALLORGE into the phytosociological studies on the continent of Europe. He still insists that the formation should not be regarded as a unit of sociological classification superior to the association, but as a plant community, of any size whatever, characterized by some particular growth form (ground form) or by a homogeneous physiognomy. In other words, the formation is the growth form or biological form of the association. While no finished scheme of classification of sociological units has been attempted, he sees in BRAUN-BLANQUET's "sociological progression" a principle which may form the basis of a natural system of classification. At present "the association" and the "element" are regarded as being respectively the lowest and highest units in such a system, the latter, as defined by BRAUN-BLANQUET, being the authochthonous and permanent vegetation of a phytogeographical region.

The phytosociological terms most in use by the Zurich-Montpellier school in the French and German languages have been collected and defined by two of its leaders,[12] and in an extensive critical abstract TANSLEY[13] has added the nearest English term in current use except where the French and English terms are practically identical. This has not only enriched our ecological terminology, but also has tended to clarify our discussions by isolating and defining certain concepts that had formerly but a vague and indefinite existence.

Among the terms commonly used in the characterization of species and in the analysis of plant associations are: (1) abundance (l'abondance, Abundanz), the relative number of individuals; (2) dominance (la dominance, Deckungsgrad, Arealprozent), the extent of surface occupied; (3) distribution (la fréquence, Verteilungsart), the manner in which individuals are distributed in the population; (4) sociability (la sociabilité, Geselligkeit), the disposition of individuals in the interior of an association; (5) prosperity (la vitalité, Gedeihen), the extent to which a species completes its cycle of development in a given population; (6) periodicity (la périodicité), the seasonal duration of a species; and (7) dynamic behavior or genetic coefficient (comportement dynamique, bedingende Verhalten), the part played by the species in the development of the community. Different degrees of the various qualities are indicated numerically, or, in the case of the last, by a set of conventional

[11] PAVILLARD, J., L'association végétale: Unité phytosociologique. Montpellier. pp. 12. August 1921.

[12] BRAUN-BLANQUET, J., and PAVILLARD, J., Vocabulaire de sociologie végétale. Montpellier. pp. 16. July 1922.

[13] TANSLEY, A. G., Methodology: the new Zurich-Montpellier school. Jour. Ecol. 10:241–248. 1922.

signs. The chief terms to denote synthetic characters are: (1) constancy (la constance, Gesellschaftsstetigheit), depending upon the number of sample areas of the association in which the species occurs; and (2) fidelity or exclusiveness (la fidélité, Gesellschaftstreue), the degree to which the species is confined to the association. Five degrees of these two qualities are recognized. Other terms which have been more widely used and more commonly understood are also included in this useful list.—GEO. D. FULLER.

Ecological importance of vapor tension deficit.—Recognizing that atmospheric humidity is the most important factor in the control of transpiration and hence of plant distribution, SZYMKIEWICZ[14] has emphasized the importance of expressing this factor in terms of vapor tension deficit. He shows that the range of vapor tension deficit more nearly measures the effect of humidity upon loss of water by plants than does relative humidity or loss from the open pan evaporimeter. He also demonstrates that the maximum vapor tension deficit for the driest month of the year seems to limit the distribution of various tree species in Poland and Russia.—GEO. D. FULLER.

Dipsacus as a carnivorous plant.—CHRISTY[15] has included *Dipsacus sylvestris* in the list of carnivorous plants. The method is entirely different from that observed in the better known carnivorous plants. The cups formed by the leaves contain liquid derived from falling rain or dew, ranging in amount from half to three-quarters of a pint. This liquid seems to contain "some sweet toxic substance which attracts and stupifies many small creatures, while the structure of the cups is such as to facilitate their capture, drowning, and putrefaction, leading ultimately to the absorption by the plant of the resulting highly nitrogeneous product."—J. M. C.

Rice disease.—NISIKADO and MIYAKE[16] have investigated *Helminthosporium Oryzae*, which causes one of the most series rice diseases in Japan. It attacks all parts of the plant, and can also infect a great many other grasses. The germ tubes enter either through the stomata or by breaking through the epidermal cells by means of appressoria formed at the tips. The susceptibility of the conidia to various chemicals was tested, and it was concluded that some of them may serve to disinfect the seed and prevent the disease. The vitality of the fungus in culture extended to thirty-one months.—J. M. C.

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[14] SZYMKIEWICZ, DEZYDERY, Sur l'importance du déficit hygrométrique pour la phytogéographie écologique. Acta Soc. Bot. Poloniae 1:1–11. *figs.* 4. 1923.

[15] CHRISTY, MILLER, The common teasel as a carnivorous plant. Jour. Botany 61:33–45. 1923.

[16] NISIKADO, Y., and MIYAKE, C., Studies on the Helminthosporiose of the rice plant. Ber. Ohara Inst. Landw. Forsch. 2:133–195. *pls.* 3–9. 1922.